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Volume XIV *Number 1*

December, 1961

BUTLER UNIVERSITY

INDIANAPOLIS, INDIANA

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A PRELIMINARY STUDY OF THE CROSSING RELATIONSHIPS OF *CAPSICUM BACCATUM*[1]

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INTRODUCTION

The common bird pepper or *chilipequin* is a variable species ranging from the southern United States throughout Central America into Colombia. It has generally been assumed that this pepper was first described by Linnaeus in his *Mantissa* of 1767 under the binomial *Capsicum baccatum,* although Hunziker (1958) in his synopsis of the genus apparently does not accept this interpretation. While some authors have treated this taxon as a distinct species, others have considered it a variety of *C. frutescens* (Irish 1898) or as a variety of *C. annuum* (Smith and Heiser 1957). Hence, it seemed desirable that a study be undertaken to contribute to an understanding of the diverse forms of *C. baccatum,* both to each other and to other species within the genus.

MATERIALS AND METHODS

Thirty-nine different collections of *C. baccatum* were grown for this study, and the six races enumerated in Table I represent different morphological types used in the crossing program. One strain each of nine other species (Table I) were used in crosses with *C. baccatum.* Flowers were emasculated and all operations were carried out in an insect-free greenhouse. Pollen counts were determined by staining the grains with lactophenol blue. Pollen counts of the species listed in Table I range from 60 to 90% fertile. Chromosome counts showed all of these plants to be diploid ($N = 12$).[3]

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[1] Condensed from a thesis submitted in partial fulfillment of the requirements for the degree of Master of Arts at Indiana University, June, 1960.

[2] The author is indebted to Dr. Charles B. Heiser, Jr. who directed this research.

[3] Specimens of all parent plants and hybrids are deposited in the herbarium of Indiana University.

TABLE I

Sources of *Capsicum* species employed in crossing studies

Species	*Number*	*Collector*	*Location*
C. annuum L.	Cu27	C. B. Heiser 3346	Turrialba, Costa Rica
C. baccatum L.	Cb1	C. B. Heiser 3286	Avery Isle, La.
C. baccatum L.	Cb5	P. Alvin	Tabasco, Mexico
C. baccatum L.	Cb8	C. B. Heiser 3839	Guatemala City, Guat.
C. baccatum L.	Cb18	C. B. Heiser 3520	Turrialba, Costa Rica
C. baccatum L. (X?)	Cb22	C. B. Heiser 3462	Moravia, Costa Rica
C. baccatum L.	C36	I. Kelly	Vera Cruz, Mexico
C. cardenasii Heiser & Smith	U1	P. Smith Ac1793	La Paz, Bolivia
C. chacoense Hunziker		P. Smith Ac1848	La Pampa, Argentina
C. chinense Jacq.	CA5	P. Gonzales	Lima, Peru
C. frutescens L.	T1	Burpee "Tabasco"	Burpee Seed Co.
C. galapagense Heiser & Smith		P. Smith Ac1501	Galapagos Islands, Ecuador
C. microcarpum Cav.	C69	P. Smith Ac1005	Oruro, Bolivia
C. praetermissum Heiser & Smith	C72	P. Smith Ac1231	Piracicaba, Brazil
C. sp.	CA1	D. C. Webster	Jamaica, British West Indies

Infraspecific crosses of Capsicum baccatum. Nine reciprocal hybrid combinations were readily secured between strains listed in Table I. The pollen counts of the forty hybrids tested ranged from 25 to 90% fertile with a mean of 57%.

Interspecific crosses of C. baccatum with several other species. Capsicum baccatum X *C. annuum* L. Reciprocal crosses were attempted with Cb1, CB8, and Cb5; all were successful. Pollen counts ranged from 21 to 81% fertile with a mean of 57% for the ten plants studied.

Capsicum baccatum X *C. chinense* Jacq. Crosses were successful with Cb1, Cb5, Cb8, and C36 as the female parents. The reciprocal crosses all failed to produce seeds. For the eight hybrids studied, pollen counts ranged from 15 to 91% fertile, with an average of 54%.

Capsicum baccatum X *C. chacoense* Hunziker. Reciprocal hybrids were secured with Cb1, Cb5, Cb8, and C36. Pollen counts ranged from 0 to 41% fertile with a mean of 18% for thirteen plants. Another plant which appeared to be a hybrid produced 84% stainable pollen, but this plant was lost so that verification of its hybrid nature could not be made.

Capsicum baccatum X *C. frutescens* L. Reciprocal hybrids were secured with Cb1, Cb5, and Cb8; hybrids were also obtained with C36 as the male parent, but the reciprocals failed. Pollen counts of the ten hybrids ranged from 0 to 83% fertile with a mean of 35%.

Capsicum baccatum X *C. sp.* The species employed in this cross has not yet been satisfactorily identified. It closely approximates the description given by Dunal (1852) for *C. cerasiforme.* The fruit is within the size range of *C. baccatum* but in the form of a cherry. Reciprocal hybrids were secured with Cb1, and Cb5. Using Cb8 and C36 as the female parents, hybrids were produced, but the reciprocals of these combinations failed. Pollen counts of the hybrids ranged from 7 to 32% fertile with a mean of 19% for 12 hybrids.

Capsicum baccatum X *C. cardenasii, C. galapagense, C. microcarpum,* and *C. praetermissum.* No hybrids were secured with the exception of Cb8 crossed with *C. microcarpum,* where seedlings were produced which died shortly after germination. Seeds were formed in several crossed with *C. praetermissum,* but all were inviable.

RESULTS

The chief value of these crosses is in demonstrating that it is possible to secure hybrids of *C. baccatum* with several *Capsicum* species and impossible to secure them with others. However, it must be pointed out that these results are based on only one representative for all the species other than *C. baccatum.* Considerable diversity is encountered in several species of *Capsicum;* such that it seems reasonable to refer to these as species complexes. It is with reservations that any conclusions may be drawn regarding the fertility of the hybrids based on the results of pollen counts. During the course of the study it was found that there was some variation in pollen counts depending on the season of the year during which pollen samples were collected. Soria (1958) has found that tropical species of *Solanum* show variation in fertility when grown under different day lengths. Detailed studies of seed set were not made, but it was observed that all of the hybrids produced some fruit with viable seeds. Most of the fruits produced by the hybrids of *C. baccatum* X *C. chacoense* were devoid of seed. It is clear, however, that there is a close genetic relationship among the members of the *C. baccatum* complex, and that there seems to be an equally close relationship between *C. baccatum* and *C. annuum.* The pollen fertilities of hybrids with *C. chinense* were nearly as high as those with *C. annuum,* but it may be significant that the reciprocals failed in this case.

Although it is not possible to establish *C. baccatum* as a species on the basis of these crosses alone, there does seem to be sufficient evidence for regarding it as a species based on morphological findings. The following description of the species is formulated from the study of thirty-nine different living collections grown under uniform field conditions supplemented with the study of collections from several herbaria.

Capsicum baccatum L. Plants .3 to 1.5 m tall, branches numerous, rather slender, fastigiate, flexuose, frequently purple striate, glabrous or sparingly pubescent, leaf blades 30-130 cm long, 20-80 cm wide, ovate-acuminte, abruptly narrowing into petioles; peduncles solitary; calyx cyathiform, truncate, subentire or with obscure teeth; corolla rotate to slightly campanulate, greenish-white, unspotted, less than 1.5 cm in diameter with lobes 5-7 mm long and sinuses 1-5 mm deep; fruit subround or ovate, rarely somewhat elongate, about 7-8 mm in diameter, unripe fruit blackish-spotted to almost entirely black, becoming red at maturity. No single character is in itself sufficient to distinguish this taxon from closely related species, but the combination of characters is usually effective. The black color of the immature fruit seems to be a consistent and useful character although neglected by previous investigators.

DISCUSSION

Whether natural hybridization occurs was not determined by the present investigation; however, it is clear from the results secured here that such hybridization might well be expected with species having a sympatric distribution. Heiser has collected plants in Costa Rica that may represent hybrids with *C. annuum* and possibly with *C. frutescens* and *C. chinense.*

During the course of this investigation seeds of a plant similar to *C. baccatum* (Fig. 1) collected at Key Largo, Florida, were received from Dr. Monroe Birdsey. A single seed from this collection germinated and gave rise to a plant (KL1) that proved to be tetraploid ($N = 24$). Since this count is based on a single specimen, one cannot be certain whether the tetraploid number is characteristic of a whole population or whether it represents a single aberrant individual. However, it is the first report of a natural polyploid in this genus. All attempts to cross the tetraploid with various strains of *C. baccatum* as well as with other species were unsuccessful.

LITERATURE CITED

Dunal, Felix, 1852. Solanaceae in A. de Candolle. Prodromus. *3*:422.

Hunziker, A. T. 1958. A synopsis of the genus *Capsicum*. International Congress of Botany, Rapports et communications par venus avant la congress. 18th Congress: 73-74.

Irish, H. C. 1898. A revision of the genus *Capsicum* with especial reference to garden varieties. Ann. Mo. Bot. Gard., 9th rep.: 53-110.

Smith, P. G. and C. B. Heiser, Jr. 1957. Breeding behavior of cultivated peppers. Proceedings of the American Society for Horticultural Science. *70*:286-290.

Soria, J. 1958. Study of relationships between certain tropical species of the *Solanum nigrum* complex. Ph.D. thesis. Indiana University Library.

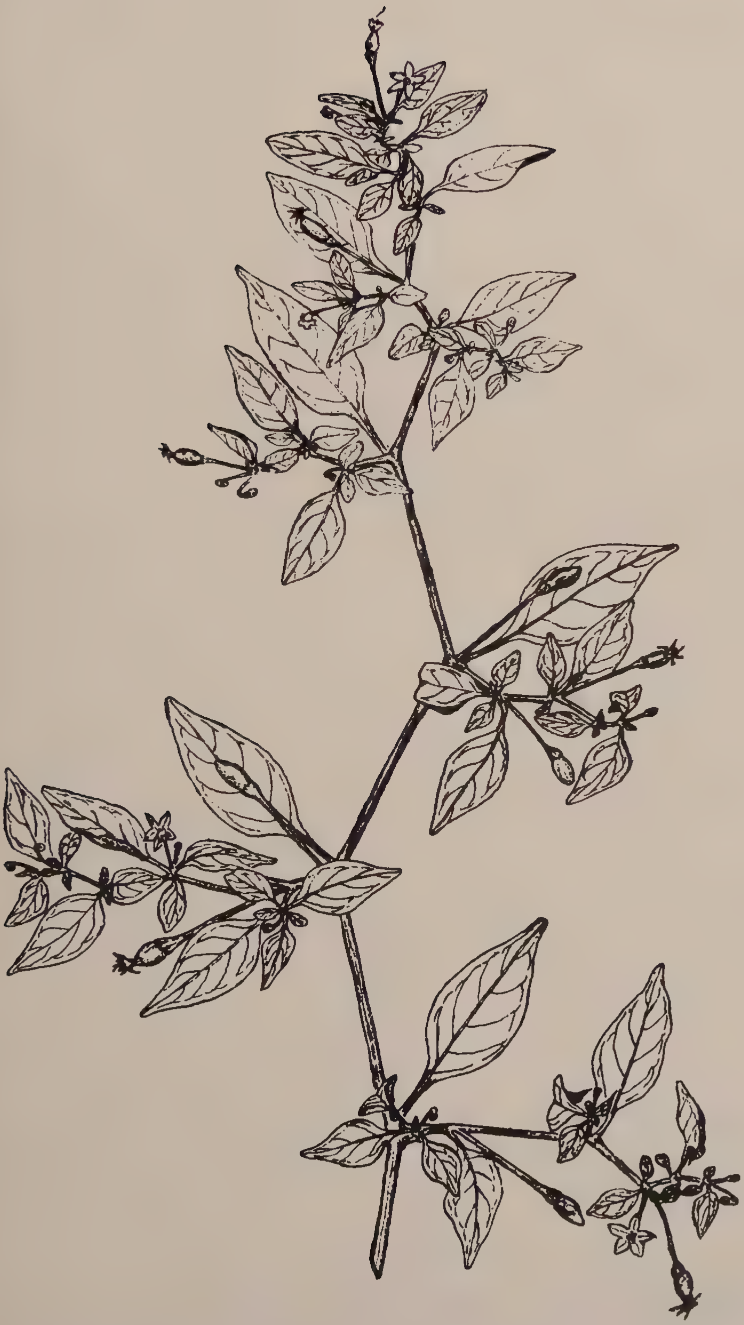

FIG. 1. Drawing of a naturally occurring *Capsicum* tetraploid (KL1) from Florida.

THE GENUS *SPHAERELLOPSIS* IN INDIANA

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A new alga was recorded for Marion County in the State of Indiana in May, 1960, when a sample of water from a small fish pond on the property of Professor William Cupp, near the Butler University campus, was found to contain a large number of individuals of *Sphaerellopsis fluviatilis* (Stein) Pascher (1927). No previous report of the occurrence of this genus in Indiana is listed in the flora records of the state.

The presence of *Sphaerellopsis fluviatilis* (Stein) Pascher in California was reported by Smith, 1933. Since this first report of its occurrence in the United States, it has been reported to exist in Ohio by Lillick and Lee, 1934. In 1954 this organism was reported by Forest as occurring in a river in Tennessee.

Sphaerellopsis is a unicellular member of the Order Volvocales of the Division Chlorophyta. It differs from members of the genus *Chlamydomonas* in being surrounded by a persistent gelatinous sheath that differs in shape from the protoplast. The cell with its sheath is entire and individuals in this collection appear to be sub-spherical. The protoplast is elongate and fusiform with two equally long flagella, an anterior eyespot and two contractile vacuoles. The chloroplast is massive and bears a single pyrenoid.

Some asexual reproductive stages were present in the Indiana material. Here the gelatinous sheath of the mother cell persisted around the daughter protoplasts with each of the new individuals surrounded by its own sheath.

Size of the vegetative cells varied from 14-30 microns in length and 10-30 microns in width.

No sexual reproduction was observed but according to Pascher it is isogamous.

Specimens of *Sphaerellopsis fluviatilis* (Stein) Pascher have been placed in the Butler University Herbarium.

LITERATURE CITED

Forest, H. S., 1954. Handbook of Algae. University of Tennessee Press, Knoxville.

Lillick, L. and Lee, I. 1934. Check List of Ohio Algae. Am. Mid. Nat. 15 (6): 715-751.

Pascher, A. 1927. Die Susswasser-flora Deutschlands, Osterreichs und der Schweiz. Heft 4. Gustav Fischer. Jena.
Smith, G. M. 1933. The Fresh-water Algae of the United States. McGraw-Hill, New York.

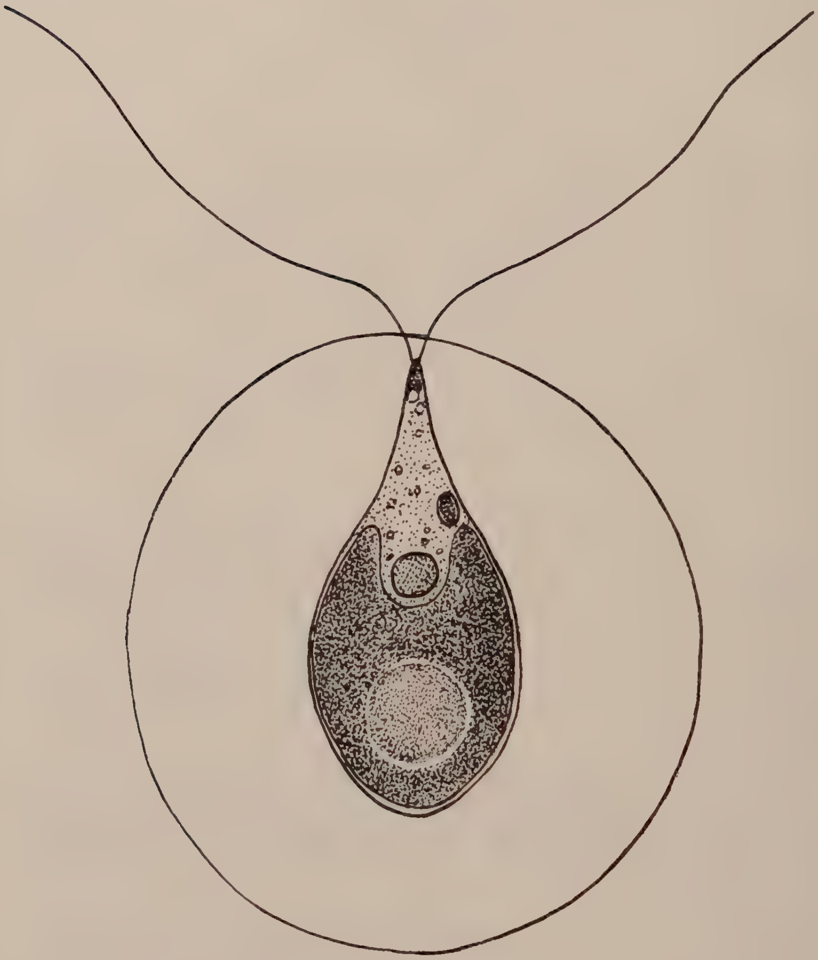

FIGURE I

Cell of *Sphaerellopsis fluviatilis* (Stein) Pascher (x2000).

HYBRIDIZATION BETWEEN *JUNIPERUS ASHEI* BUCHHOLZ AND *JUNIPERUS PINCHOTI* SUDWORTH IN SOUTHWESTERN TEXAS[1]

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INTRODUCTION

This paper presents an analysis of the interactions of two processes, hybridization and differential selection, in the diversification of *Juniperus* where *Juniperus Ashei* Buchholz and *Juniperus Pinchoti* Sudw.[3] occur together. An attempt is made to show man's influence toward accelerating these interactions.

Since the taxonomist is rarely blessed with a natural population which is undifferentiated and the time to watch it go through the throes of evolutionary processes, he must usually work with messy, complex populations and speculate upon historical factors to visualize simpler patterns. In the meantime he must untangle the mosaic of forces and events which have determined the population currently under study. While much has been said about the importance of this factor or that factor in speciation, most naturalists sense that populations of races or species result from the interaction of mosaics of forces and events acting in different combinations and different degrees throughout the various taxonomic groups.

Three major processes, distinct in both operation and result, which may act on a population either simultaneously or successively are inbreeding, differential selection, and hybridization.

Inbreeding, an event producing divergence following spatial isolation, is an important cause of abrupt isolation of segments of an originally undifferentiated population. The separation may be of great magnitude as in those species showing discontinuous distributions in Japan and North America (Asiatic-American disjuncts, Asa Gray, 1846, 1859; A. J. Sharp;

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[1] This research was supported by a grant, G-2948, from the National Science Foundation.

[2] Now in the Department of Botany at Vanderbilt University.

[3] *Juniperus Pinchoti* Sudw. This name is used here in the sense that it is the southern facies or "variety" of *Juniperus monosperma* Sarg. The origin and significance of *J. Pinchoti* is complex and will be presented elsewhere.

1952); or a matter of a few feet either horizontally or vertically as in the snails, *Achatinella* (J. T. Gulick, 1905) and *Partula* (H. E. Crampton, 1916, 1932) in the Pacific; and the synusial isolation of mosquitos in Trinidad (C. S. Pittendrigh, 1948). Isolated colonies may result from numerous agents: for instance, climatic and topographic changes; disoperations by man such as overgrazing, clearing, and fire; successional mosaics moving toward a climax association; or disjunct dissemination. Gene interchange is restricted with the possible consequent random fixation of non-adaptive characters in small colonies. *Iris setosa* Pall. var. *canadensis* Foster, endemic to eastern Canada, was derived from a small colony of plants isolated from the main body of *Iris setosa* by continental glaciation (E. Anderson, 1936a). Similarly, random fixation has effected pigment genes in the South Sea island bird, *Pachycephala pectoralis* (E. Mayr, 1932). Differential selection seems to be another important force acting on isolated colonies but to produce divergent evolution of adaptive characters, a seemingly acceptable explanation of the odd behavior of sectional characters in *Vernonia* (H. A. Gleason, 1923) where adaptive diversity is great though apparently unrelated to ecologic or physiologic factors. The *Vernonia* pattern is surely the result of the isolation of colonies after expansion by migration. The patterns of racial or even specific differentiation resulting from inbreeding, while not uncommon in other plants, are not evident in *Juniperus*.

The second factor, differential selection, produces divergence consequent to environmental adaptation. Where genotypes persist in the face of the production of abundant hybrid progeny, it is by the selective advantage of the adapted genotypes and the elimination of the hybrids. Numerous ecotypes, races, and species are able to proliferate and evolve because of their tight adaptation to a particular habitat. In *Tradescantia* many species are interfertile and remain distinct because of differences in ecological adaptations (E. Anderson and K. Sax, 1936, and E. Anderson, 1936b). *Tradescantia ohiensis* Raf. is found on open sunny cliff tops among prairie species while *T. subaspera* Ker grows in shady, moist woods at the cliff bases. They may come in contact occasionally along talus breaks where they freely mix. *Juniperus Ashei* Buchholz and *J. virginiana* L. are confined to specific rock strata in the stony lands of the Arbuckle Mountains in Oklahoma, but hybridize freely where the rubble of these strata mix (Hall, 1952a). The leopard frog, *Rana pipiens,* forms a cline correlated with temperature gradients in eastern North America where the terminal forms are so diverged as to have lost interfertility, (J. A. Moore, 1944, 1947). Whether distribution is clinal or discontinuous depends on the pattern of the limiting environmental factors. Species may show clines for one character and ecotypic discontinuities for another. The "niche effect" demonstrates similar complex variability factor by factor.

Adaptive divergence may result in isolation of populations within species. Where isolating mechanisms are active, clines may eventually be replaced by discontinuities.

The third factor, antithetic to differential selection, is hybridization. It may result in swamping partial discontinuities between divergent populations through the resumption of gene interchange. This return of gene flow is usually the result of a rather catastrophic change in the environment, most frequently man induced. After hybridization between adapted races or species there is further elimination of hybrid genotypes poorly adapted to habitat conditions and increase for those hybrids suited to the disturbed habitat. Populations seem to go through states of tightening up from the effects of differential selection to a loosening from hybridization. Thus evolution both conserves efficiency and produces new trials for achieving new efficiency as changes occur in the environment.

THE HABITAT

The distribution of *Juniperus Ashei* (Hall, 1954) was shown to be a narrow ellipse about 1,000 miles long roughly running from southwestern Missouri to central Coahuila along a northeast, southwest axis. In the northeast the species is disjunct and shows strong introgression from *J. virginiana;* in Coahuila it is again disjunct. The main body of the species, *J. Ashei,* occurs in the Central Texas Section and the Edwards Plateau[4] of Texas. Along the western margin of the range of *J. Ashei* from Saltillo, Mexico, north to the Pecos River and east to about Abilene, Texas, there is abundant evidence of introgression into *J. Ashei* of genes from *J. Pinchoti.* Population samples were made along a curving transect from Dryden, Terrell County, north to Big Spring, Howard County, and east to Abilene, Taylor County, and northwestward to the Palo Duro Canyon, Texas. Further samples of *J. Pinchoti* were collected west across the Trans-Pecos of Texas to determine the extent of introgression in that direction of genes from *J. Ashei.* The massive limestones of the Comanche series[5] from the Cretaceous have been essentially exposed to plant colonization since their seas were drained and their formations were uplifted. The Upper Cretaceous Woodbine merely licked at the northern edge of these massive strata and the recent Gulf invasions likewise never reached as far north as the Balcones fault. These massive aquifers were probably covered with the uniform vegetation characteristic of the Tertiary and developed the more arid modern aspect as a consequence of the changes wrought by the Laramide Revolution which culminated in the Pliocene. The evidence suggests that while the Edwards Plateau was at its highest, *J. Ashei* may have been well isolated from other juniper species. The first species to have contacted *J. Ashei* seems to have been *J. virginiana* from the north and east (Hall, 1952b). Much later, apparently post-settlement, contact was made between *J. Ashei* and *J. Pinchoti* from the west. A wealth of supporting evidence is available from early landholders of the region.

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[4] The physiographic provinces after N. M. Fenneman, Physiography of Western United States, McGraw Hill, New York, 1931.

[5] The geologic formations referred to in this paper are described in The Geology of Texas, Vol. I, Stratigraphy by E. H. Sellards, W. S. Adkins, and F. B. Plummer, Un. of Tex. Bull. 3232, 1932.

Typical *J. Ashei* is restricted to the thick limestone aquifers from the Balcones Escarpment on the east to the western edge of the high cap from Ranger to Abilene to a few miles south of Barnhart and Rankin to Sheffield and the eastern breaks of the lower Pecos River. *J. Pinchoti* is most abundant on the Permian clays and sands above and below the Callahan Divide and on the clayey conglomeritic or caliche Cretaceous lowlands from San Angelo to Rankin and westward. The two species occur in mixed stands and produce hybrid swarms on the talus of the high escarpment and in limy washes of the lower Pecos breaks from Sheffield to Del Rio. Their habitat requirements are quite distinct. Ashe's juniper requires a good supply of soil moisture, freedom from grazing or browsing damage, a limy substrate, and low competition pressures from grasses. *J. Pinchoti* requires less soil moisture and withstands grazing or browsing pressure easily because of its bud crown. It grows in sand or clay, and competes well with grasses. Like buffalo grass and mesquite, *J. Pinchoti* may occur in playa lakes where its roots survive low oxygen tension.

REVIEW OF MORPHOLOGY

Juniperus Ashei and *J. Pinchoti* are not only in the Sabina section (fleshy berry-cones and scale leaves) but in the same species group (*occidentalis*). Thus one expects rather slight differences in at least several characters. Both species are monospermous with denticulate leaf margins. Both are multi-stemmed xerophytes with *J. Pinchoti* expressing the extreme form in both characters. However, the differences are greater than meet the eye on casual inspection or from studies of only herbarium materials. By contrast these two species are very different in their ecology. *J. Ashei* grows mostly in calcareous soils over aquifers or limy rock talus while *J. Pinchoti* grows in a variety of soil types from sands to heavy clays where it may compete with grasses once germination has been accomplished. Essentially, all junipers require exposed soil for effective germination and seedling survival.

FIG. 1 shows the comparative gross morphology of *Juniperus Ashei* and *J. Pinchoti.*

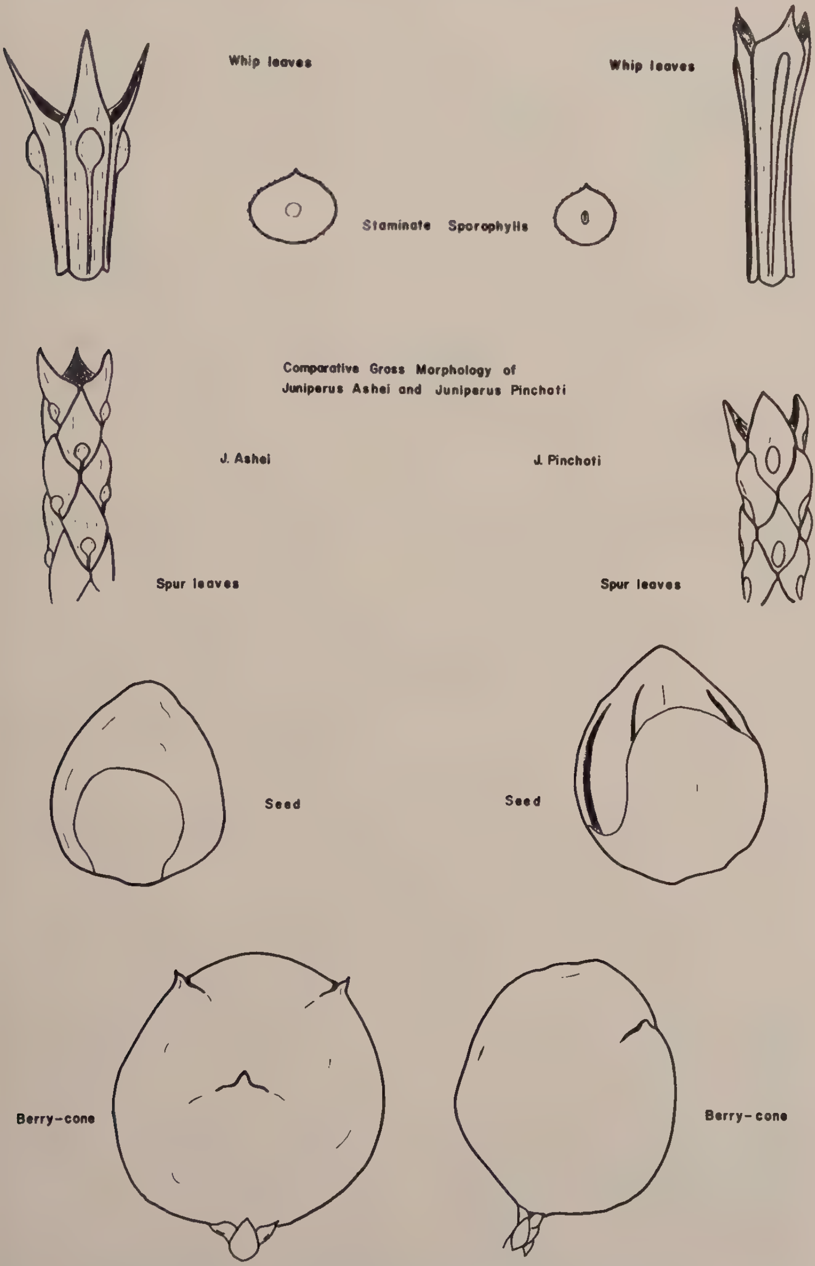

FIG. 1. Comparative gross morphology of *Juniperus Ashei* and *J. Pinchoti.*

TABLE 1 summarizes the major morphological differences between the two species:

JUNIPERUS ASHEI	JUNIPERUS PINCHOTI
1. Trunk more or less branched above the base, typically a foot or more above the ground level; without bud crown; aspect generally bush-like, often as tall as or taller than wide; height to 35 feet.	1. Trunk branched at or below the ground level; with bud crown; aspect a spreading dwarf, wider than tall; height to 15 feet.
2. Angle of branching of laterals obtuse; branches numerous and uniformly increasing in length back from the tip giving a rounded effect.	2. Angle of branching of laterals acute; branches less numerous and uniformly short back to an occasionally quite long lateral giving a strict wand-like aspect.
3. Foliage dense, mostly ternate, even on ultimate branches, but finer textured than *J. Pinchoti.*	3. Foliage dense, ternate, more coarse in texture.
4. Foliage olive-green, young woody whip bright rust-brown at base changing to dull tan to olive-green at tip.	4. Foliage a lighter, brighter yellow-green. Young woody whip pinkish-red at base changing to orange to yellow-green at tip.
5. Whip leaves average 7 mm. long with a circular raised gland (about ½ mm. in diameter), and a keel extending from the gland to the base of the sheath.	5. Whip leaves average 8 mm. long with a flat, very long, knifeline gland usually the entire length of the leaf, frequently lateral glands 1 to 3 mm. long result in a leaf with triple glands, no keel.
6. Spur leaves 1½ to 2 mm. long, with round gland or frequently eglandular, a slight hinge where blade joins sheath, occasionally a keel.	6. Spur leaves 2 to 2½ mm. long, with flat elliptic or almost round obscure gland or eglandular, no hinge, no keel.
7. Fruit large (6-8 mm. in diameter), resinously aromatic-pungent, azure-blue, slightly bloomy, with slightly resinous juicy pulp, which is black when fresh and rust-brown when dry, fruiting branchlets straight.	7. Fruit slightly smaller (4-7 mm. in diameter), with a mild raw pumpkin odor, rust-brown to rust-red, with thin dry fibrous pulp, greenish when fresh, pale tan when dry, fruiting branchlets straight.
8. Seed chocolate-brown, 5 mm. in length, 1, rarely 2 per berry-cone, sharply pointed conical tip, no pits, occasionally a very narrow longitudinal groove, smooth white hilum covering at least one-fourth the length of the seed.	8. Seed medium tan, 5-6 mm. long filling the fruit tightly, 1, occasionally 2 per berry-cone, blunt to slightly shovel-like tip usually with several narrow longitudinal grooves to the tip, smooth elliptic less distinct hilum covering one-half to two-thirds the length of the seed.

FIG. 2 shows the diagrammatic growth habit and branching pattern in these two junipers. From the axis to the ultimate branchlets, branching achieves the seventh degree in *J. Ashei* and the eighth degree in *J. Pinchoti,* which is the greatest degree known in *Juniperus*. In *J. Ashei* the arrangement of the ultimate branchlets is fairly uniform about the twigs giving a full-rounded aspect, while in *J. Pinchoti* the ultimates tend to branch predominately in one plane producing a fan-like aspect. In the eastern part of the range of *J. Pinchoti,* especially near the edges of the Cretaceous escarp-

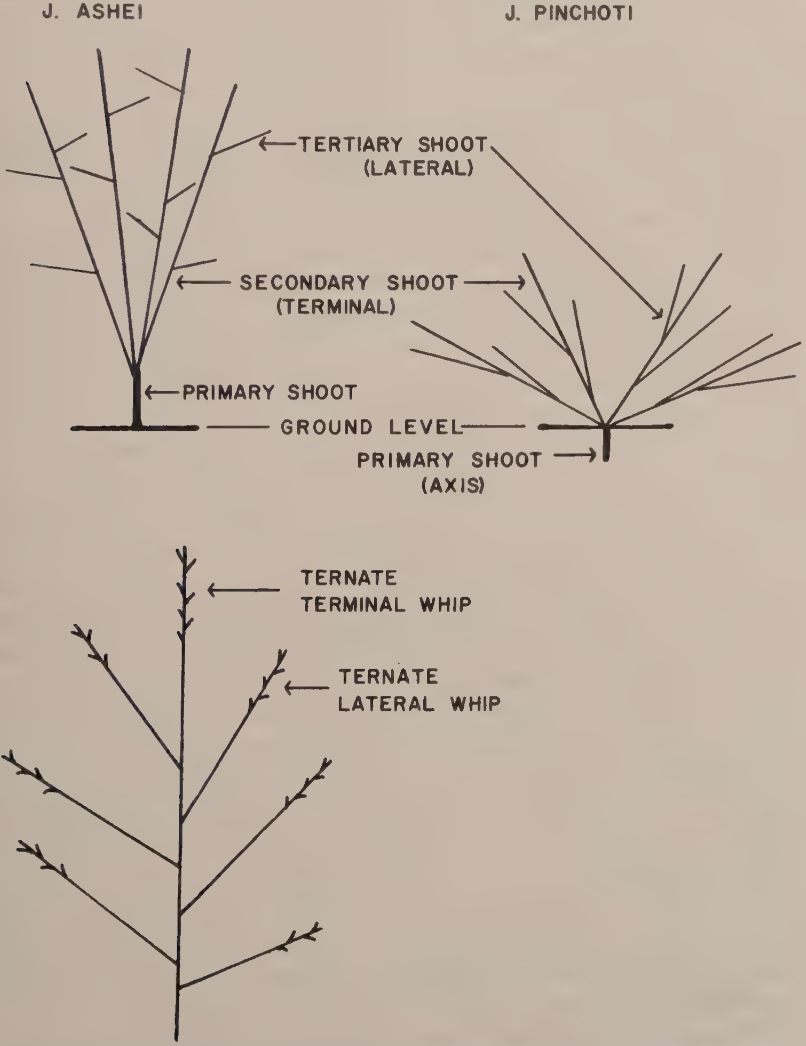

FIG. 2. Above, a diagrammatic representation of growth habit and branching pattern in *Juniperus Ashei* and *J. Pinchoti*. Below, a secondary shoot (terminal) enlarged, for identifying terminology.

ments, the branching tends to resemble that of *J. Ashei.* This is the area where hybrids between the two junipers are common. Farther westward the branching of *J. Pinchoti* becomes more and more fan-like, resembling that of *J. Deppeana* Steud.

The secondary shoot of Fig. 2 shows its morphology and identifies the terminology used with respect to it in this paper. Terminal whip is the long shoot growth which is characterized by long type leaves and borne at the apex of the secondary shoot (second degree of branching). Lateral whip is long-shoot growth at the apex of the tertiary shoot (third degree of branching). The whip is apparently wholly ternate in these two species. The leaves shown in Fig. 1 represent those from typical specimens of *J. Ashei* and *J. Pinchoti.* The long leaves are whip-leaves characteristic of long-shoot growth which occurs terminally on secondary and tertiary shoots. The short leaves are spur-leaves characteristic of short-shoots. While recombinations of leaf characters in the hybrids suggest moderate linkage, they are so distinct as to be readily observed among mixed populations. Again, *J. Ashei* exhibits slightly greater apical dominance with its suppression of lateral long-shoots even though the mass of tissue produced per unit is nearly the same. One may distinguish between the two junipers by the greater terminal and lateral whip of *J. Pinchoti* over *J. Ashei.* There are several variable quantitative characters which differentiate these junipers even though no single key character is dependable.

METHODS

The Population Samples. Analyses of variability for *Juniperus Ashei* have been presented elsewhere (Hall, 1952a, 1952b, 1955). This species shows introgression with *J. virginiana* at the eastern edge of its range along the Balcones Escarpment and northeastward into the Ozark Plateau. Hundreds of population samples have been taken and measured throughout the range of *J. Ashei.* Population 1 of Fig. 3 shows variability of *Juniperus Ashei* from the Central Texas Section and the Edwards Plateau contrasted with the variability of *J. Pinchoti* (Population 13) from the Pecos Valley and High Plains sections of the Great Plains Province. Both species, *Juniperus Ashei* and *J. Pinchoti,* have been sampled and six characters measured throughout the species ranges. This paper is concerned with the region where the two species clearly influence one another. The area of mutual influence is between the 98° and 105° longitude, 29° N to 36° N latitude. This region was covered thoroughly and samples taken wherever juniper populations were substantial. Where plants were sparse, transects over several miles were made. Sample size varied from eight specimens to one hundred specimens with an average of thirty specimens per stand. Even though each stand was studied as a whole only healthy plants of the same age class were measured. Collections were made by a wandering L- transect to sample sites varying in topography.

The secondary shoot (FIG. 2) was selected as the most useful material for characterizing variability. Shoots were selected with similar orientation and for their value in characterizing the whole plant. A length of 45 cm. from the tip was chosen as most suitable to give an accurate measure of branching pattern as shown by the angles, lengths, and amount of whip of the tertiary branches. The reliability of the secondary shoot characters was thoroughly discussed in previous papers (Hall, 1952a, 1952b).

Character Analysis. In the stands sampled standardized photographs (to scale) were taken to show variation in habit. The sex was recorded since these are dioecious species. Site factors for each sample were noted in the field books. The following characters were measured for use in scatter diagrams and for further statistical treatment: 1. gland length-width ratio for whip leaves, 2. distance from tip of gland to tip of leaf, 3. length of whip leaf, 4. length of terminal whip (secondary shoot), 5. length of lateral whip (sum of whip on tertiary shoots 45 cm. from the tip of the secondary), 6. berry-cone diameter.

Four of these characters were selected to construct scatter diagrams and population indices: gland length-width ratio, lateral whip length, terminal whip length, whip leaf length. Thirteen populations were selected to show the distribution of variation involving *J. Ashei* and *J. Pinchoti.* These populations are diagrammed in FIGURES 3, 4, and 5.

In woody plants, aspect or habit is frequently a capricious character. However, branching pattern, the relative lengths, positions, and angles of the lateral branches and the branching degree are excellent characters of diagnostic value even in hybrid swarms. Edgar Anderson and Marion T. Hall have made numerous analyses of branching pattern in woody plants: sweetgum, red, sugar, and black maples, hackberry and sugarberry, and several of the shrubby dogwoods. My students and I have analysed branching pattern in *Juniperus* and *Pinus.* These analyses are very useful in showing affinities and recombinations among species groups. They are also easily and accurately accomplished. FIG. 4 shows selected specimens from a hybrid swarm between *J. Ashei* and *J. Pinchoti* in the Pecos watershed between Dryden and Sheffield, Texas. These diagrams are scale drawings of secondary shoots (see FIG. 2) collected from comparable branches of plants of the same age class. The branching patterns of juniper species were carefully studied first to determine what unit would characterize most species. Intra-individual as well as inter-individual variability was determined. A secondary shoot no less than 45 cm. in length was determined to be adequate to characterize the southwestern species. For *Juniperus* these branch-

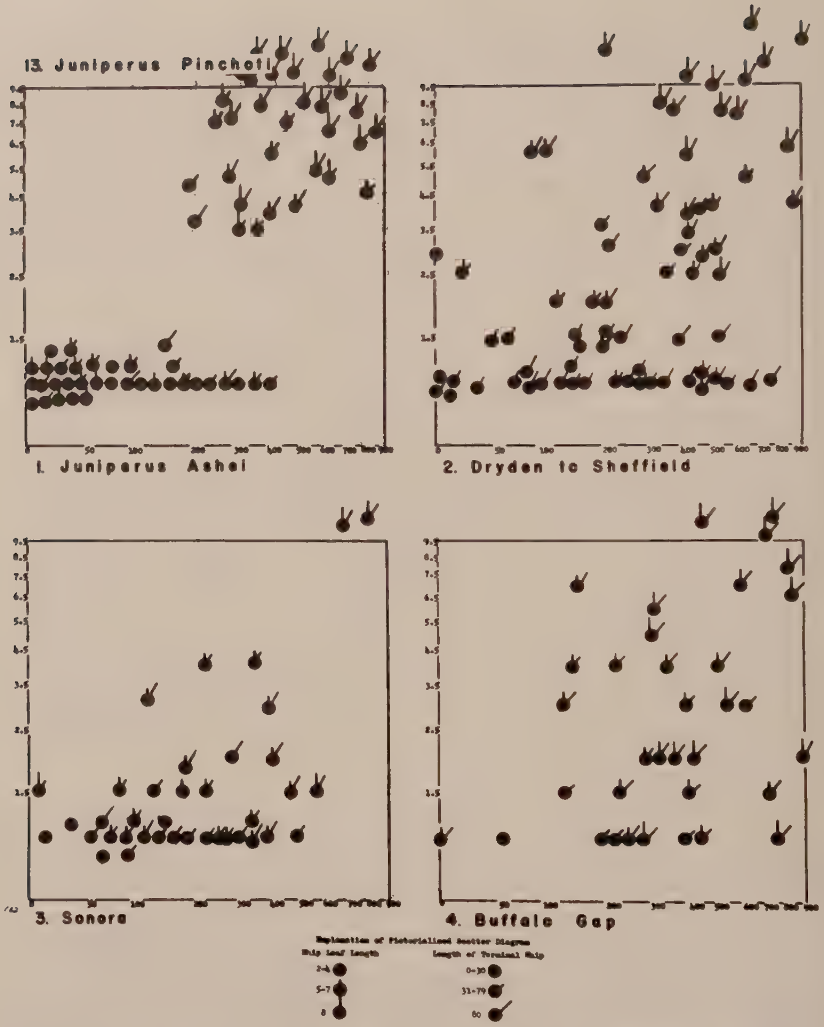

FIG. 3. Pictorialized scatter diagrams of selected populations of *Juniperus Pinchoti* introgressed by *J. Ashei* in central and west Texas. Populations 2, Dryden, Terrell County; 3, Sonora, Sutton County; 4, Buffalo Gap, Taylor County, Texas.

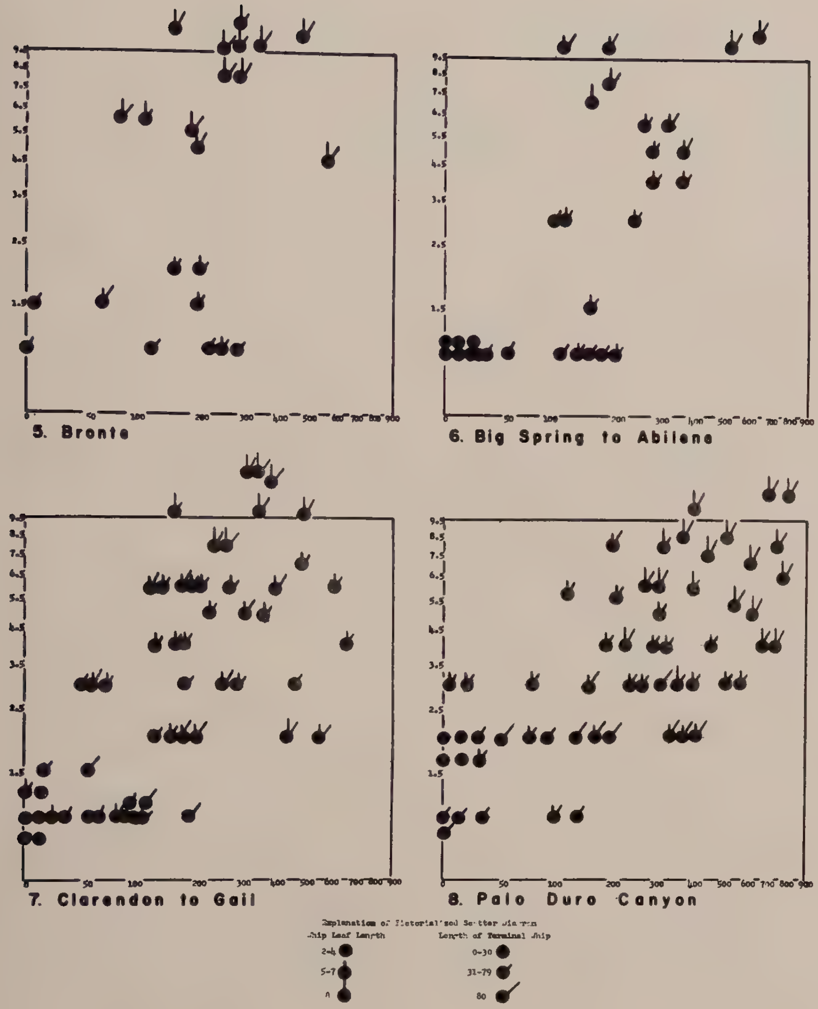

FIG. 4. Pictorialized scatter diagrams of selected populations of *Juniperus Pinchoti* introgressed by *J. Ashei* in central and west Texas. Populations 5, Bronte, Coke County; 6, Big Spring, Howard County; 7, Clarendon, Donley County; 8, Palo Duro Canyon, Randall County, Texas.

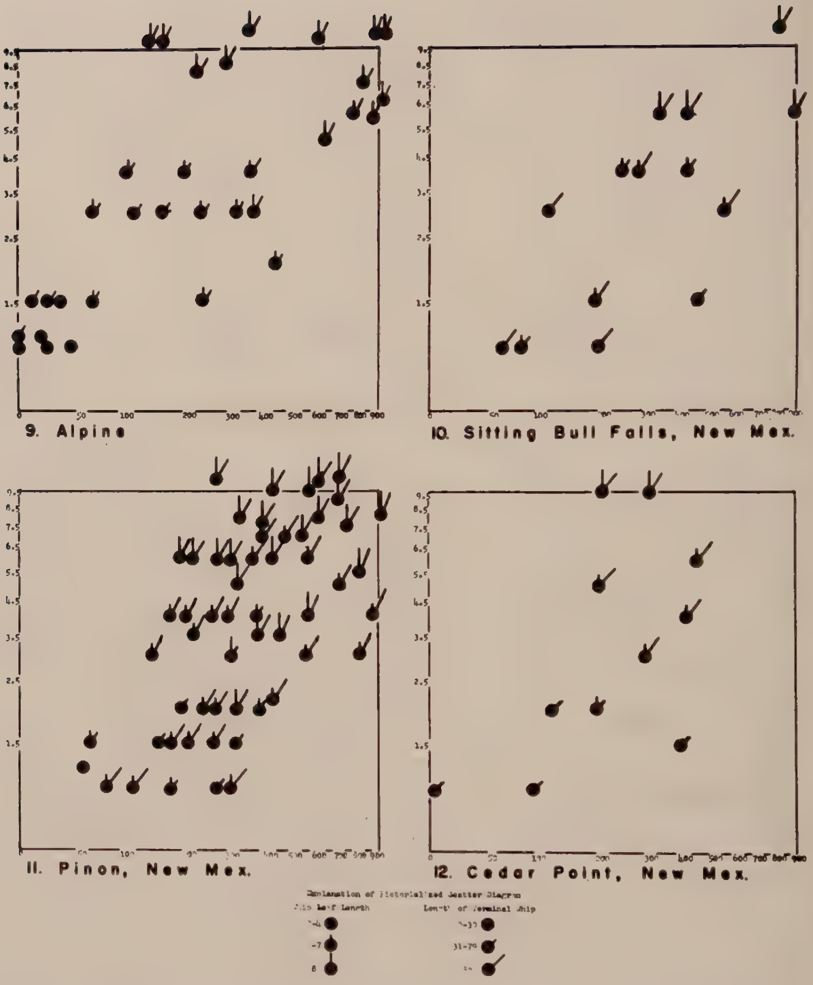

FIG. 5. Pictorialized scatter diagrams of selected populations of *Juniperus Pinchoti* introgressed by *J. Ashei* in west Texas and southeastern New Mexico. Populations 9, Alpine, Brewster County, Texas; 10, Sitting Bull Falls, Eddy County, New Mexico; 11, Pinon, Otero County, New Mexico; 12, Cedar Point, Chaves County, New Mexico.

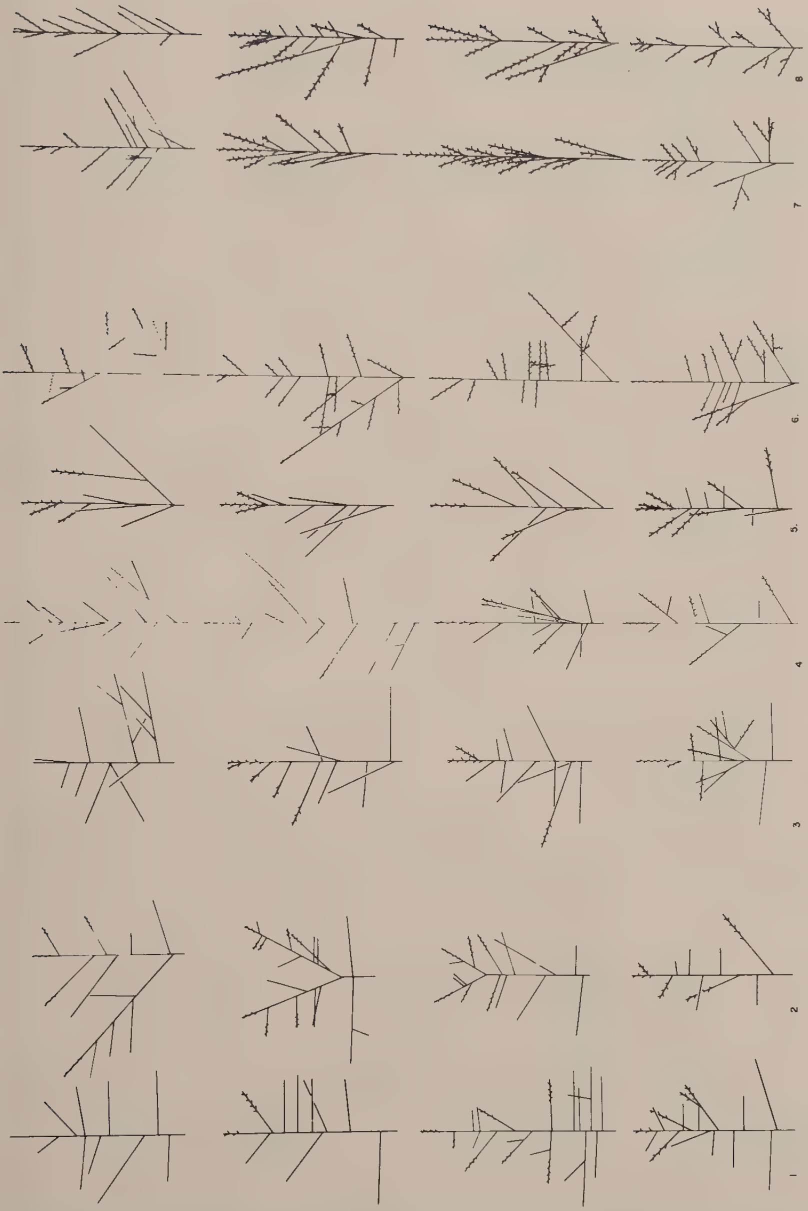

Fig. 6. These diagrams represent the terminal 45 cms. of secondary shoots (see Fig. 2) of *Juniperus Ashei* and *J. Pinchoti*. The two lower rows, 1 and 2, are *J. Ashei;* the two upper rows, 7 and 8, are *J. Pinchoti;* the four middle rows, 3, 4, 5, 6, are hybrids of the two species.

ing pattern diagrams show six characters: length of tertiary branches, relative spacing of tertiaries, angles of tertiaries, amount of long shoot growth on secondaries, amount of long shoot growth on tertiaries, arrangement of leaves (decussate vs. ternate) on secondaries and tertiaries. Where these characters differ between species, they show such clearly marked recombination patterns in the hybrids to be powerful indicators of affinity to the hybridizing species. Wide recombinations also suggest weak linkage of multiple factors, an impression supported by the spread of characters in the scatter diagrams. The branches of rows 1 and 2, Fig. 6, are to be referred to *J. Ashei,* even though when compared with *J. Ashei* farther east on the Edward's Plateau, these Pecos River specimens suggest some introgression from *J. Pinchoti.* The four middle rows (3, 4, 5, 6) are from hybrid individuals, the third row are individuals resembling *J. Ashei* in these characters, while the sixth row are those closer to *J. Pinchoti.* Branches of rows 7 and 8 are specimens to be referred to *J. Pinchoti,* even though they show quite strong introgression from *J. Ashei* in the lower Pecos breaks.

RESULTS

The pictorialized scatter diagrams (Figs. 3, 4, 5) show that hybrid swarms between *J. Ashei* and *J. Pinchoti* are well developed from the lower Pecos to Abilene and the Callahan Divide in Texas. Introgression of genes of *J. Pinchoti* are not evident eastward on the summit of the Comanche and Edward's Plateaus where *J. Ashei* is quite homogeneous. However, the introgression of genes of *J. Ashei* westward is another story. The variation spectrum shows some measurable *J. Ashei* influence as far west as the Davis Mountains of Texas north through the Guadaloupe to the flanks of the Sacramento Mountains of New Mexico. However, actual *J. Ashei*-like specimens are rarely found so far westward. Farther north introgression of *J. Ashei* genes are measurable only east of the Pecos Valley along the breaks of the Llano Estacado until they disappear north of Caprock, New Mexico, well south of the Canadian River watershed.

Populations 5, 6 (Fig. 4) show that differential selection is powerfully working on these hybrid populations. The habitats vary with almost knife-line discontinuities, and the populations they support are equally discontinuous though highly variable. Even as far southwest as the Glass Mountains of west Texas, limy moist habitats support hybrids of *J. Ashei* and *J. Pinchoti* very close to the former species while tight, dry clay soils support more typical *J. Pinchoti.* Wherever the habitats are clearly mixed or possess more gradual ecotones, whether at the base of the Comanche Plateau or in the foothills of the Sacramento Mountains over three hundred miles westward, the whole hybrid spectrum between *J. Ashei* and *J. Pinchoti* occurs with large numbers of intermediates. These two species and their hybrids present a beautifully clear example of the effects of differential selection by the habitat on a complex gene pool.

Analysis of the population behavior of the six characters diagrammed in FIG. 6 likewise supports the results stated above.

The map, FIG. 7, shows the extent of this mutual influence between *Juniperus Ashei* and *J. Pinchoti*. Populations 1, *Ashei* and 13, *Pinchoti* are as "pure" stands of the species as may be found. Populations 2 through 12 show varying amounts of introgression between the species.

A more detailed examination of each population in FIGS. 3, 4, 5 clearly show certain significant features concerning the interactions of the two species.

Numerous hybrid swarms at the commissures of the ranges, introgression of Ashe's juniper into Pinchot's juniper clearly measurable as far west as the Palo Duro Canyon and Alpine, Texas, weakly measurable to the Sacramento Mountains of New Mexico, are evidences that there are at most only slight barriers to hybridization between these species. Recombinations are wide and yet linkage is sufficient to show a strong tendency for the characters of the species to stay together. Hybrids, close to Ashe's juniper, with

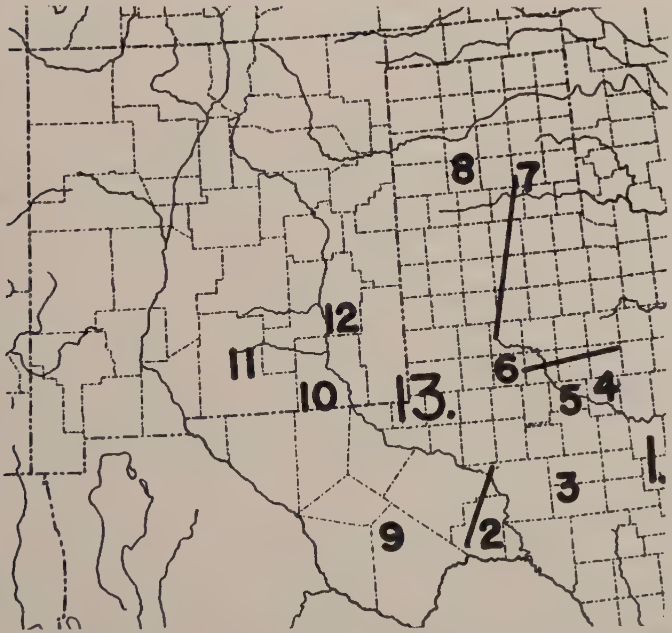

FIG. 7. Distributions of Populations 1 through 13 of Figs. 3, 4, and 5. The inked line represents transect collections. Population 1 is *Juniperus Ashei;* 13 is *J. Pinchoti;* 2 through 12 are populations of *J. Pinchoti* introgressed by genes from *J. Ashei.*

wide angles of branching, also show reduced whip, with few long lateral branches, a tendency for keeled leaves and rounded raised glands while hybrids closer to Pinchot's juniper have acute branching, much whip, numerous long but widely spaced lateral branches, flattened leaves with long narrow ruptured glands. The best developed hybrid swarms are in regions where the species meet with the most favorable soil, moisture relationships. The largest colonies of hybrids are in the breaks on talus and alluvium of the lower Pecos River from Sheffield to Dryden. The talus and alluvium are not only fine reservoirs but are also heavily calcareous in this area. The breaks of the upper Devils River have similar stands but with fewer numbers of *J. Pinchoti* variants. Hybrid swarms are numerous along the talus of the north slopes of the Cretaceous cap to San Saba and the Llano uplift. Hybrid swarms are missing in the Permian from San Angelo, Ballinger, and Paint Rock but develop extensively again about the Callahan Divide from Blackwell to Cross Plains. Here again the Cretaceous talus mixes with the Permian clays and presents a hybrid habitat which supports a broad spectrum of recombinants. Populations 2 (Dryden on the breaks of the lower Pecos,) 3 (Sonora on the breaks of the upper Devils River), and 4 (Buffalo Gap on the Callahan Divide) are seen to be well developed hybrid swarms in well "mixed" habitats. The best development of the *J. Pinchoti* element in the hybrid swarms is in the areas where the rainfall is low enough for the soil factors and topography to become limiting to *J. Ashei.* The Dryden stands (Population 2, Fig. 3) have an 18 inch rainfall with rugged terrain going from hilly talus to rocky limestone streambeds to fairly level clay hardpan areas. Here *J. Ashei* and close recombinants occupy the talus, the limestone washes and streambanks where moisture is normally plentiful. *J. Pinchoti* and recombinants occupy the clayey flats while mixing where the habitats intergrade. This is a very easily observed differentiation after one has learned the junipers. Westward from the lower Pecos the rainfall drops off rapidly so that these areas, such as the Glass Mountains near Alpine (Population 9, Fig. 5) where good talus accumulations are too dry (14 inches) for typical *J. Ashei,* support close recombinants of that species in rocky limestone creekbeds and banks. In dryer areas westward from Alpine (10 to 12 inches) *J. Pinchoti* shows little influence from *J. Ashei* except in more mesic canyons or mountain talus in localized situations (Populations 10, 11, 12 of Fig. 5).

Near Sonora, Texas, the Comanche limestones (Fredericksburg group) form the cap and slopes of the uplands overlooking narrow clayey valleys formed from the Walnut group of rocks. Permian clays are some fifty miles to the north. At Sonora in the Devils River breaks we have a well developed population of *J. Ashei* and introgressants with *J. Pinchoti.* Habitats suitable for more extreme forms of *J. Pinchoti* are restricted, and there are very few such specimens (Population 3, Fig. 3). This area supports an average annual rainfall of 22-23 inches.

The Callahan Divide supports large numbers of hybrids. *J. Ashei* grows on the mesa tops in Cretaceous limestone soils and on the slopes and colluvial limy material near the bases of the dissected plateau. Farther out, to the north or the south, in the Permian clays, *J. Ashei* disappears and *J. Pinchoti* becomes abundant. At the edges of the divide where the habitats are mixed the hybrids are very numerous. The stand discussed in this paper from the Divide is labelled Buffalo Gap (Population 4, Fig 3). The average annual rainfall at the Buffalo Gap is 24 inches, the most mesic habitat presented in this paper. There is a vigorous growth of *J. Ashei* where the individuals are closely spaced and show well developed whip. *J. Pinchoti* is likewise vigorous, and the hybrids are numerous showing a full spectrum of recombinations.

Where habitats are sharply contrasting the intermediates between *J. Ashei* and *J. Pinchoti* are missing or infrequent. At Bronte in Permian clays of the rough lands of the Colorado River watershed, *J. Pinchoti* is abundant. Where intermittent streambeds drain from the nearby Cretaceous knolls *J. Ashei* recombinants are found. The distribution of juniper in such a site is weakly bimodal with the intermediate spectrum of hybrids poorly developed or missing. The habitat differences, from limy streambed to clayey valley floor, are almost knifeline, and these junipers segregate accordingly (Population 5, Fig. 4). In areas where "parental" habitats do not mix, selection is a powerful force tending to keep the species distinct, yet allowing some introgression.

The stands occurring in Triassic and Permian but close to the Cretaceous cap, from Big Spring to Trent to Abilene, (Population 6, Fig. 4) show a similar pattern as those in the Permian at Bronte. *J. Ashei* recombinants are found in limy streambeds while *J. Pinchoti* recombinants are found on the clayey valley slopes. The average annual rainfall varies from 20 inches at Big Spring to 24 inches at Abilene, enough to support *J. Ashei* where other conditions are suitable.

Farther west in the Glass Mountains northeast of Alpine where the whole landscape is formed from Permian limestones and conglomerates, there are again fairly well developed intermediates between *J. Ashei* and *J. Pinchoti.* Habitat selection is not favoring only the recombinants close to the species. Even here the specimens close to *J. Ashei* are found in the streambeds and those close to *J. Pinchoti* on the rough uplands, a moisture response. Intermediates are relatively numerous. Westward from Alpine, *J. Pinchoti* shows little influence from *J. Ashei.*

To the northwest of the Callahan Divide, hybrid swarms occur along the caprock where limy Cretaceous talus mixes with the calcareous and gypseous Dockum group (Triassic) or where the talus rubble is well charged with water drained from the caprock as in the upper Palo Duro Canyon. The average annual rainfall varies along the caprock from the head of the Palo Duro where it is 24 inches to Big Spring where it is 20 inches. A transect study of junipers along this caprock (Clarendon, Population 7, FIG. 4) shows *J. Ashei* introgressants in the more mesic areas and numerous intermediates in the area as a whole. However, when one collects westward on the Cenozoic above the caprock little influence from *J. Ashei* is evident in the occasional specimens of *J. Pinchoti.* The major differences in the stands below the caprock from those of the Callahan Divide is the lower vigor and wider spacing of individuals in the more western stands and the lack of quite typical specimens of *J. Ashei* even though close introgressants are not difficult to find.

The upper Palo Duro Canyon (State Park area, Population 8, FIG 4) shows introgression of *J. Ashei* into *J. Pinchoti,* but the juniper populations are much more complex here because of the presence of genes of *J. virginiana* and *J. scopulorum.* A more detailed analysis of variability in *Juniperus* in the Palo Duro Canyon will be reported elsewhere.

Populations 10, 11, FIG. 5 show slight influences from *J. Ashei* genes. These are stands from low summits or mountain talus where soil moisture is more favorable for *Ashei* genes than the intervening desert scrub and grasslands. These stands are further complicated by genes from *J. Deppeana* and will be given a more detailed discussion elsewhere. Population 12 represents the farthest northwest that *Ashei* influence is descernible in stands of *J. Pinchoti.*

Study of these populations (FIGS. 3, 4, 5) show that hybridization and differential selection have played a dynamic role in the development of the southwestern junipers. Unpublished data of the authors' for other southwestern and Mexican species of *Juniperus* suggest the same point.

DISCUSSION

Where internal barriers are weak which is usually the situation where allopatric species are concerned, introgression results in races which grade imperceptibly and smoothly into the parent species (but does not show clinal gradients for different characters); i.e., the closer one approaches the parent species the less easily can morphological evidence of introgression be observed. But where differential selection is strong these dispersed introgressant genotypes "clump together" to form discontinuous ecotypes and sympatric speciation becomes incipient, and internal differentiation within that species is given new impetus. The degree of discontinuity of these ecotypes is a function of the discontinuities of the operational environment which is great in arid areas, less so in mesic areas.

The examples from this paper suggest the complexity which may arise from divergence consequent to environmental adaptation through the agency of hybridization. This is certainly a very general phenomenon able to stamp its influence in whatever degree over great distances.

Indeed, our general experience leads us to the conclusion that racial or specific differentiation in response to selection pressure, i.e., ecotype differentiation, is indeed widespread. Perhaps most natural populations of species undergo this type of stimulation at some stage of their existence. It seems evident that the development of a vigorous gene pool is the experience of most species which are situated in open, rapidly changing habitats. As communities close and the efficiency of the utilization of environmental resources increases the population tends to become either depauperate of biotypes, or perhaps more generally biotypically stabilized. Although adapted and efficient in its own time, a species may depend on its close relatives for rejuvenation, through hybridization, at a future time of radically changing environmental conditions.

SUMMARY

1. *Juniperus Ashei* of central Texas and *J. Pinchoti* in western Texas hybridize where they meet to form hybrid swarms and introgress as far west as the Palo Duro Canyon, and Alpine, Texas.

2. *J. Ashei* is the more mesic species occupying aquiferous limestones; *J. Pinchoti* occupies dry clayey lowlands where it may successfully compete with grasses.

3. Hybrid swarms are best developed in intermediate habitats where the species meet, e.g., Dryden, Sheffield, Texas, upper Devils River, and at the Callahan Divide from Blackwell to Cross Plains, Texas.

4. Introgression of genes of *J. Ashei* into *J. Pinchoti* is measurable from the western Edward's Plateau becoming progressively lower in intensity to the western slopes of the Sacramento Mountains of New Mexico.

5. Bimodal variation is typical of stands growing in habitats where nearly knifeline differences are observed. Where limestone washes (intermittent) with clayey banks sloping to clayey talus support junipers, variants close to *J. Ashei* occupy the limy creekbed, while those close to *J. Pinchoti* occur on the clay slopes. Differential selection in these habitats is quite strong.

6. The results of hybridization and differential selection between these species are marked ecotypic differentiation, enhancement of variability, and increase in survival value as evidenced by recent expansions of stands of introgressants.

ACKNOWLEDGEMENTS

Our sincere thanks go to George Sprugel, Jr., Environmental Biology Division Director, National Science Foundation, for his efficient aid. It is with gratitude that we acknowledge gifts of research equipment from Annette and Stephen Stackpole, Grosse Pointe Shores, Michigan. We are grateful to Barton H. Warnock for his hospitality and his extensive knowledge of the Trans Pecos of Texas. Thanks go to Ray Jackson, Chester Rowell, Jack Hughes, and Boone McClure for making available herbarium records, for specimens, and for notes on the history of land use in the high plains. Special thanks go to Rex Webster and Ron Wathen for field assistance throughout the study.

LITERATURE CITED

Anderson, Edgar. 1936a. The species problem in *Iris*. Ann. Mo. Bot. Gard. *23:* 457-509.

______. 1936b. Hybridization in American *Tradescantias*. Ann. Mo. Bot. Gard. *23:* 511-525.

Anderson, Edgar, and K. Sax. 1936. A cytological monograph of the American species of *Tradescantia*. Bot. Gaz. *97:* 433-476.

Crampton, H. E. 1916. Studies on the variation, distribution, and evolution of the genus *Partula*. The species inhabiting Tahiti. Carnegie Inst. Wash. Publ. *228:* 1-311.

———. 1932. Studies on the variation, distribution, and evolution of the genus *Partula*. The species inhabiting Moorea. Carnegie Inst. Wash. Publ. *410:* 1-335.

Fenneman, N. M. 1931. Physiography of western United States. McGraw Hill, New York.

Gleason, H. A. 1923. Evolution and geographic distribution of the genus *Vernonia* in North America. Amer. Jour. Bot. *10:* 187-202.

Gray, Asa. 1846. Analogy between the flora of Japan and that of the United States. Amer. Jour. Sci. and Arts *52:* 135-136.

———. 1859. Diagnostic characters of new species of phaenerogamous plants, collected in Japan by Charles Wright, with observations upon the relations of the Japanese flora to that of North America, and other parts of the northern temperate zone. Amer. Acad. Arts and Sci. Mem. *6:* 377-452.

Gulick, J. T. 1905. Evolution, racial and habitudinal. Carnegie Inst. Wash. Publ. *25:* 1-269.

Hall, Marion T. 1952a. A hybrid swarm in *Juniperus*. Evol. *6:* 347-366.

———. 1952b. Variation and hybridization in *Juniperus*. Ann. Mo. Bot. Gard. *39:* 1-64.

———. 1954. Nomenclatural notes concerning *Juniperus*. Rhodora *56:* 169-177.

———. 1955. Comparison of Juniper populations on an Ozark glade and old fields. Ann. Mo. Bot. Gard. *42:* 171-194.

Mayr. Ernst. 1932. Birds collected during the Whitney South Sea expedition. Amer. Mus. Novitates *20:* 1-22; *21:* 1-23.

Moore, J. A. 1944. Geographic variations in *Rana pipiens* Schreber of Eastern North America. Bull. Amer. Mus. Nat. Hist. *82:* 345-369.

———. 1947. Hybridization between *Rana pipiens* from Vermont and eastern Mexico. Proc. Nat. Acad. Sci. *33:* 72-75.

Pittendrigh, C. S. 1948. The Bromeliad-Anopheles-Malaria complex in Trinidad. I.—The Bromeliad Flora. Evol. *2:* 58-89.

Sellards, E. H. et al. 1932. The geology of Texas, Vol. I. Stratigraphy. Un. of Tex. Bull. 3232.

Sharp, A. J. 1952. *Tovara* in Mexico. Rhodora *54:* 305-306.

A KEY AND ANNOTATIONS FOR SOME CHARACEAE COLLECTED IN WYOMING

FAY KENOYER DAILY
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and
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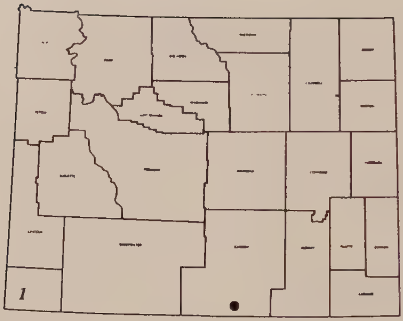
University of Wyoming

A number of specimens of the Characeae collected by C. L. Porter and Marjorie Porter have been added to the Rocky Mountain Herbarium, University of Wyoming. Duplicates of these as well as the extant collections there were made available to the senior author for study. Distribution maps and ecological data were also supplied. A few collections from other sources were added.

Thirteen taxonomic categories were distinguished as being represented in these specimens representing three genera and eleven species. The finding of a new variety of the rare species, *Tolypella hispanica,* marked the first record of a dioecious *Tolypella* in the United States. It was also found that some charophytes infrequently reported for the United States were represented as follows: *Chara longifolia* Robinson, *Chara hirsuta* Allen, *Nitella acuminata* ssp. *glomerulifera* A. Br., *Nitella opaca* Ag., *Chara zeylanica* f. *inconstans* (Kütz.) H. & J. Groves. Some common charophytes represented were *Nitella flexilis* (L.) Ag., *Chara contraria* A. Br. ex Kütz., *Chara vulgaris* Vaill. ex L., *Chara globularis* Thuill. and the somewhat less common *Chara delicatula* Ag.

Wyoming is located in northwestern United States of America between 41° and 45° latitude. Elevation ranges from 3,100 to 13,785 ft. above sea level. Life zones include the low plains and fertile river valleys, high sagebrush and grassy plains, basal slopes of the mountains, middle mountain slopes, a narrow subalpine zone in the timberline region, and the arctic-alpine mountain peaks and crests above the timberline. Its boundaries contain the western part of the great plains, high desert plateaus and mesas of the intermountain west cut by deep canyons or walled by high mountains, and the continental divide. The soils where charophytes were found chiefly range from the stony soils of the mountains, to the fertile river valleys, bogs and glacial drift. The waters range in temperature from the cool alpine aquatic habitats to hot springs (32° C. for a spring in which *Chara* was growing).



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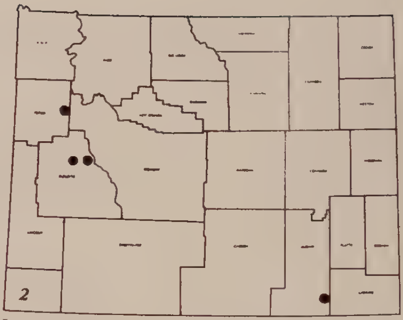

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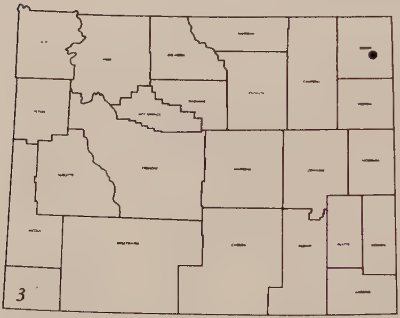

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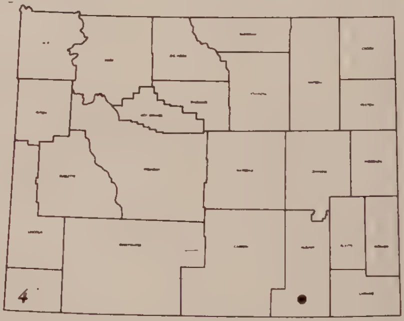

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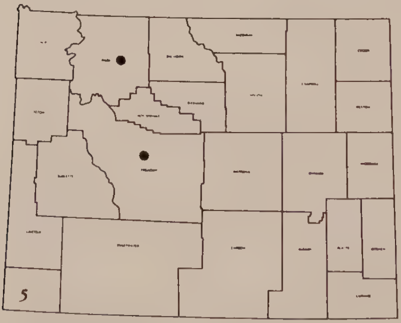

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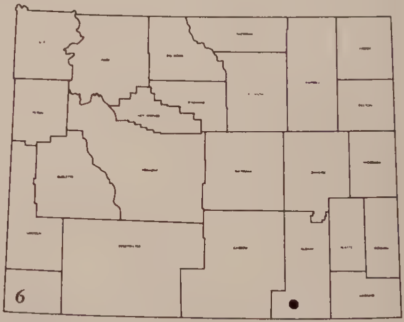

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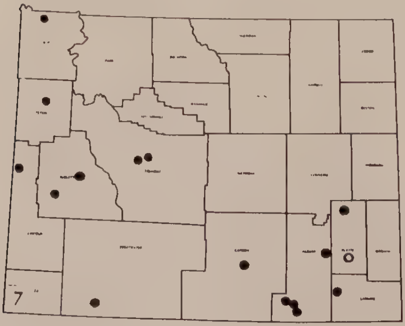

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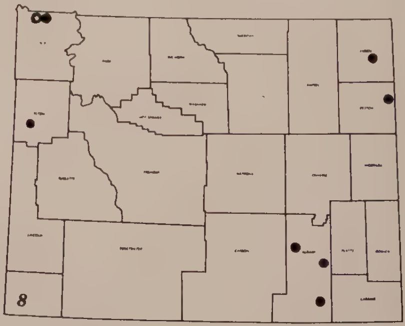

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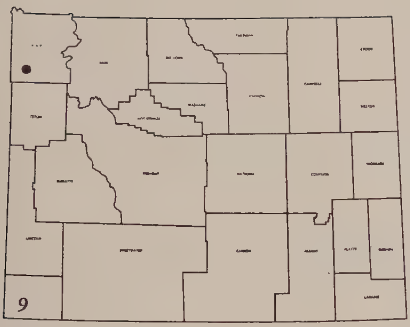
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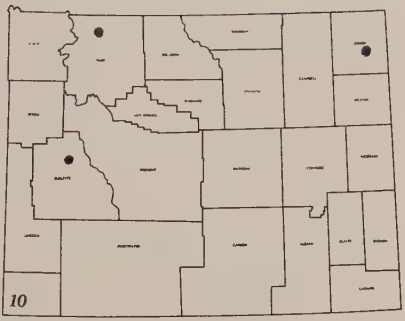
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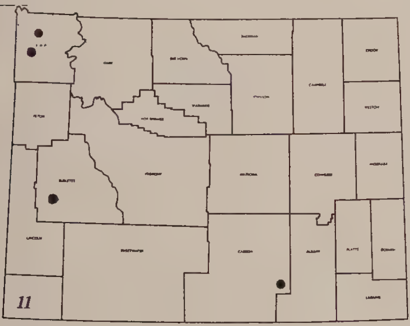
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Distribution of the charophytes of Wyoming indicated by a dot or circle at the location of a collection site. Map 1. *Nitella acuminata* ssp. *glomerulifera* A. Br. Map. 2. *Nitella flexilis* (L.) Ag. Map. 3. *Nitella opaca* Ag. Map 4. *Tolypella hispanica* var. *porteri* Daily. Map. 5. *Chara longifolia* Robinson. Map 6. *Chara hirsuta* Allen. Map 7. *Chara contraria* var. *contraria* A. Br. ex Kütz. (dot), *Chara contraria* var. *hispidula* A. Br. (circle). Map 8. *Chara vulgaris* var. *vulgaris* Vaill. ex L. (dot), *Chara vulgaris* var. *condensata* Breb. (circle). Map. 9. *Chara zeylanica* forma *inconstans* H. & J. Groves. Map 10. *Chara globularis* Thuill. Map 11. *Chara delicatula* Ag.

If the accompanying maps (Maps 1-11) showing the distribution of the charophytes of Wyoming were superimposed on a topographic map of the state, the dots and circles representing the location of collecting sites would be associated with the mountains and river systems. This reflects the recent soils and greater moisture in these areas. Although the continental Wisconsin glaciation did not reach Wyoming, glaciers formed in the mountains during this period. When they receded, they left alluvial fans, lake terraces, and stream terraces in a region of sufficient moisture with soil of sufficient essential minerals to maintain suitable aquatic habitats for charophytes. This area covers only about 10 percent of the state, with the soils of the remaining portion drier and having been subject to much leaching and erosion for many thousands of years.

In the citation of specimens, the location of collections are designated as follows: RM, Rocky Mountain Herbarium, University of Wyoming, Laramie, Wyo.; BUT, herbarium of F. K. Daily, Butler University, Indianapolis, Ind.; F, Chicago Natural History Museum, Chicago, Ill.; UC, University of California Herbarium, Berkeley, Cal.

If a collection contains a mixture of species, for instance, if a collection of *Chara contraria* also contains some *Chara globularis* this is indicated in the citation of specimens under *Chara globularis* by the phrase "with *Chara* *contraria*" under which name the collection is filed in the herbarium at Butler University.

A KEY FOR SOME WYOMING CHARACEAE

Coronula with 10 cells in two tiers	
Mature oospore laterally flattened; antheridium apical at a branchlet node	NITELLA
Ultimate ray one-celled	
Monoecious	
Tip of ultimate ray long-acuminate . . .	1. *Nitella acuminata*
Tip of ultimate ray acute	2. *Nitella flexilis*
Dioecious	3. *Nitella opaca*
Mature oospore terete; antheridium lateral and below the oogonium at a branchlet node	TOLYPELLA
Dioecious	4. *Tolypella hispanica*
Coronula with 5 cells in one tier	CHARA
Stipulodes in one series around stem	5. *Chara longifolia*
Stipulodes in two series around stem; stem corticated	
Primary cortex (with spines) alternating with short secondary cortical cells (without spines)	6. *Chara hirsuta*
Primary cortex alternating with longer secondary cells (diplostichous)	
Primary cortical cells prominent	7. *Chara contraria*
Secondary cortical cells prominent	8. *Chara vulgaris*
Primary cortex alternating with two secondary cortical ranks (triplostichous)	
First branchlet internode ecorticate.	9. *Chara zeylanica*
First branchlet internode corticate	
Stem cortex cells all about equal in diameter; stipulodes rudimentary.	10. *Chara globularis*
Stem cortex cells unequal in diameter, primary prominent; stipulodes developed	11. *Chara delicatula*

1. NITELLA ACUMINATA subsp. GLOMERULIFERA Braun. Abh. Kön. Akad. Wiss. Berlin (1882): 39, Plate 4, fig. 88. 1883.

For descriptions and illustrations see Allen (2, p. 43, fig. 45), and Braun *loc. cit.*

Only a single collection (Map 1) was made in Wyoming of this rather rare subspecies. The plants were growing in shallow water of an alpine lake at 10,000 ft. elevation. They are said to occur in the pure water of ponds and ditches (Braun, loc. cit.).

Specimen seen: CARBON COUNTY: Sierra Madre near the Continental Divide, in Battle Lake, shallow water. July 14, 1953. *C. L. Porter 6325* (RM, BUT).

2. NITELLA FLEXILIS (L.) Ag. Syst. Alg., p. 124, Lund, 1824.

Descriptions and illustrations are given in Wood (10, p. 348, plate 1, 3C and plate 2, 8A), Daily (4, p. 12, plate 2A) and descriptions are in Allen (1, p. 38) and fructifications are described in Horn af Rantzien (6, p. 176, plate 2, figs. 8-14).

The distribution of this species in Wyoming (Map 2) is primarily in the mountains of the Wind River Range and one collection in the Laramie Range. Usually this species grows in streams and lakes near the inlet in deep water or in shaded and silted areas of lakes. It was found in a stream at one location in Wyoming and the possibility of shading is likely in the timbered recesses of the meadows of the Wind River Range.

Specimens seen: ALBANY COUNTY: Laramie Range, Middle Crow Creek east of Vedauwoo, 7,700 ft. In a shallow, sluggish stream. *C. L. Porter & Marjorie W. Porter 8488,* July 29, 1960. (RM, BUT). SUBLETTE COUNTY: Wind River Range, western slope, in Horseshoe Lake, in about 10 ft. of clear, cold water, 9,000 ft., August 1, 1952. *C. L. Porter 6151,* (RM, BUT); Wind River Mountains, 7 mi. due west of Fremont Peak, Lower No-name Lake, *O. H. Robertson,* August 9, 1943, (BUT). TETON COUNTY: Wind River Range near Lake of the Woods. 9,400 ft. Forming separate tufts in sandy bottom of lake in 1-3 ft. of clear water. August 8, 1956. *C. L. Porter 7198.* (RM, BUT).

3. NITELLA OPACA Ag. Syst. Alg., p. 124, Lund, 1824.

Descriptions and illustrations are given in Wood (10, p. 347, plate 1, fig. 5A, plate 2, figs. 7 B & C), Daily (3, p. 152, plate 1C), and descriptions in Allen (1, p. 37).

A single collection (Map 3) was made in Wyoming. This species is scattered over the United States and infrequently reported, usually being associated with a habitat having rock outcrops and boggy soil. In the habitat where the species was collected in Wyoming, Cretaceous shale and nearby coal deposits apparently provide the proper organic and mineral requirements.

Specimen seen: CROOK COUNTY: With *Chara globularis,* Sundance, 4,750 ft. July 8, 1896. *A. Nelson 2249a.* (RM, BUT).

4. TOLYPELLA HISPANICA var. PORTERI Daily. Butler Univ. Bot. Stud. 11:144-148. 2 pls. Nov., 1954.

Description and illustrations are given in Daily *(loc. cit.)* and the fruiting bodies of the species are described by Horn af Rantzien (6, p. 198 ff.).

Only one collection (Map 4) was made in Wyoming. Repeated attempts to find it again have failed. It was growing in a small, shallow, alkaline pond with a soft, mucky bottom (black ooze) on the Laramie plains in southeastern Wyoming. The plants formed cushion-like tufts in about 2 feet of water. The Laramie Plains are a plateau with a short growing season, but with a great deal of sunlight because of the clear air, and this is a good agricultural center.

Specimen seen: ALBANY COUNTY: Pond 7 miles southwest of Laramie. 7,200 ft. August 25, 1952. *C. L. Porter 6191.* (RM, *isotype;* BUT, *holotype*).

5. CHARA LONGIFOLIA Robinson. Bul. N. Y. Bot. Gard. 4(13): 272. 1906.

A description is given in Robinson *(loc. cit.)*

This little known species has been found in Kansas and Iowa. Indiana was also mentioned by Robinson, but this specimen has not been found. It is described as possibly appearing dioecious, but is monoecious. The material from Wyoming has only female gametangia or fructifications.

Another collection by L. Whitford came from 2-3 ft. of water in a woods pool, one mile west of the ocean, Kill Devil Hill, Dare Co., N. C.

It is uncommon in Wyoming, but forms very extensive and deep beds in 2-10 feet of murky water in large alkaline lakes at about 5,000 to 5,500 ft. in the central and northern part of the state (Map 5).

Specimens seen: FREMONT COUNTY: Ocean Lake, forming great beds in 2-10 ft. of water. 5,200 ft. in elevation. July 17, 1953. *C. L. Porter 6332.* (RM, BUT). PARK COUNTY: Alkaline lake 2 miles east of Cody. 5,000 ft. Forming extensive beds in 2-3 ft. of water. July 21, 1955. *C. L. Porter 6790.* (RM, BUT).

6. CHARA HIRSUTA Allen. Bul. Torrey Bot. Club 27 (6): 301, plates 10 and 11, June 1900.

Descriptions and illustrations are given in Allen *(loc. cit.)* and Daily & Kiener (5, p. 42, plate 1B).

Distribution (Map 6) in Wyoming is limited to the one collection. This species was known only from the type before the collection in Nebraska (Daily & Kiener, 5) where it was found in a sandhill pond and marsh pond in Sheridan County. It was originally found in some sink-hole lakes at Lakeside, San Diego County, California. The Wyoming specimen was labeled *Chara Nelsonii* Allen. No record of publication of this name nor any other herbarium specimen of it has been found, and the specimen seems to fit the above category very well so it is placed here.

Specimen seen: ALBANY COUNTY: Soda Lakes, 10 miles southwest of Laramie. 7,300 ft. September 24, 1898. *A. Nelson 5351.* (RM, BUT).

7. CHARA CONTRARIA A. Br. ex Kütz. Phyc. Germ., p. 258, 1845.

Descriptions and illustrations can be found in Daily (3, p. 158, plate 3B), descriptions in Robinson (9, p. 265) and descriptions and illustrations of the fruiting bodies in Horn af Rantzien (6, p. 260 ff., plate 12, figs. 1-11).

Distribution for Wyoming (Map 7) is in sluggish rivers, streams, ponds and lakes often forming dense beds and this is the commonest species of charophyte there. One interesting collection came from the warm water of a hot spring. Elevational range is from about 4,000-7,500 feet. This species seems to be well distributed over North America, being especially abundant in gravel pit ponds and lakes of glacial origin. Since there is a great degree of variation in this species, varietal names lose much of their usefulness and are used here only to point out the extremes of variation.

7a. Var. CONTRARIA

Specimens seen: ALBANY COUNTY: Porter Lake, in 2-5 ft. of murky water, alkaline muck bottom, 7,500 ft., July 22, 1952, *C. L. Porter 6032* (RM, BUT); small lake on Pahlo Lane, 20 miles southwest of Laramie, shallow water, alkaline muck bottom, 7,200 ft., July 26, 1953. *C. L. Porter 6348* (RM, BUT); Laramie River east of Lookout, in 2 ft. of sluggish water. 7,000 ft., July 28, 1953. *C. L. Porter 6351* (RM, BUT); Lake Hattie, in 1-3 ft. of murky water, sandy bottom, 7,200 ft., July 11, 1955, *C. L. Porter 6769* (RM, BUT); Laramie Range, Laramie River, 6,000 ft., ponds along river, July 27, 1956, *C. L. Porter 7161* (RM, BUT). CARBON COUNTY: Near Difficulty, 6,400 ft., shallow stream in arid hills, July 14, 1955. *C. L. Porter 6778* (RM, BUT). FREMONT COUNTY: Wind River, Aug. 9, 1894, *A. Nelson 796* (RM, BUT); at Diversion Dam on Wind River, 5,600 ft. in a cattail swamp, August 18, 1954, *C. L. Porter 6618* (RM, BUT); Ocean Lake, 5,200 ft., in 3 ft. of murky water, Aug. 18, 1954. *C. L. Porter 6623* (RM, BUT). LARAMIE COUNTY: Iron Mountain, Aug. 26, 1896. *A. Nelson 2738* (RM, BUT). LINCOLN COUNTY: At the north end of the Star Valley, near Thayne, 6,100 ft., small roadside ponds, July 1, 1954. *C. L. Porter 6503* (RM, BUT). PLATTE COUNTY: Platte River in the canyon, Aug. 27, 1896. *A. Nelson 2767* (RM, BUT). SUBLETTE COUNTY: With *Chara delicatula,* near Big Piney on Quintal Ranch, 6,400 ft., shallow water of a reservoir lake, Aug. 12, 1958, *C. L. Porter & Marjorie W. Porter 7638* (RM, BUT); Wind River Mountains, west flank, 21 miles NNW of Pinedale, SE ¼, sec. 26, T. 37N, R. 110W, about 5 mi. NNW of outlet of Lower New Fork Lake, spring-fed, sink-hole lake on Bill Dew Ranch, surface temperature 69° F., at about 4 ft., 57° F., Aug. 21, 1960. *Robert C. Bright* (BUT). SWEETWATER COUNTY: Along Black's Fork, about 12 miles south of Green River, 5,600 ft., alkaline stream in shallow water. July 9, 1961. *C. L. Porter & Marjorie W. Porter 8744a* (degenerate form), and *8744b.* (RM, BUT). TETON COUNTY. Two Ocean Lake. 7,000 ft. Sandy bottom, in shallow water. Sept. 2, 1956, *C. L. Porter 7241.* (RM, BUT). YELLOWSTONE NATIONAL PARK: Mammoth Hot Springs, in a pond. July 20, 1899. *A. & E. Nelson 6022.* (RM).

7b. Var. HISPIDULA A. Br.

Specimen seen: PLATTE COUNTY: Richeau Creek, 7 mi. north of Chugwater. 5,200 ft. August 19, 1959. *C. L. Porter & Marjorie W. Porter 8033* (RM, BUT).

Included here are the specimens reported as *Chara contraria, Nelson 6022* by Nelson (8) (identified by T. F. Allen); as *Chara* sp. (Nelson, 7) and *Chara foetida* (= *C. vulgaris*) (Nelson, 8), *Nelson 796* (perhaps ecorticate juvenile filaments scattered in this collection led the collector to describe this as an unusual charophyte at first); as *C. foetida* by Nelson (8), *Nelson 2738* and *2767.*

8. CHARA VULGARIS Vaill. ex L. Sp. Pl., p. 1156. Stockholm, 1753.

Descriptions are given in Robinson (9, p. 269) and descriptions and illustrations under the name *C. foetida* can be found in Daily (3, p. 160, plates 3C & 4A), and a discussion of the var. *condensata* Breb. is in Daily (4, p. 33).

Distribution (Map 8) of this species in Wyoming is in streams and boggy places. The var. *condensata* is typically found in boggy places. Elsewhere this species seems associated with habitats fed by mineral springs. Some, at least, of the habitats in Wyoming are known to be of this category. Two collections were associated with hot springs in temperature as high as 32° C. The elevational range is from about 4,500 to 7,200 ft. occurring in widely scattered locations over the state.

8a. Var. VULGARIS

Specimens seen: ALBANY COUNTY: Laramie, 7,200 ft., Sept. 7, 1896, *A. Nelson 2780* (RM, BUT); Rock Creek near Rock Dale, Aug. 21, 1897, *A. Nelson 4263* (RM, BUT); Laramie Range, canyon of the north fork of Sybille Creek, along Highway 34, 6,400 ft., in 6 in. water in sluggish places, Sept. 26, 1960, *C. L. Porter & Marjorie W. Porter 8534* (RM, BUT). CROOK COUNTY: Sundance Creek, 4,750 ft., July 6, 1896. *A. Nelson 2208* (RM, BUT). TETON COUNTY: Quaking bog, 2 miles southwest of Jackson, 6,000 ft., *J. F. Reed 2730,* Aug. 30, 1949 (RM, BUT). WESTON COUNTY: Cambria Canyon. July 29, 1896. *A. Nelson 2540* (RM, BUT). YELLOWSTONE NATIONAL PARK: In edge of Bath Lake (30-32° C.), Mammoth Hot Springs. Aug. 31, 1898. *W. A. Setchell* (UC, BUT).

8b. Var. CONDENSATA Bréb.

Specimen seen: YELLOWSTONE NATIONAL PARK: Narrow Gauge Terrace on moist path (25° C.) Mammoth Hot Springs, Aug. 31, 1898. *W. A. Setchell 1991.* (UC, BUT).

Included here are specimens reported as *Chara foetida* (= *C. vulgaris* in Nelson (8) identified by T. F. Allen, *Nelson 2208* and *2780.*

9. CHARA ZEYLANICA Willd. Mem. Acad. Roy. Sc. Berl. (1803): 86. 1805. Berlin.

A key including this form of *Chara zeylanica,* f. *inconstans*, occurring in Wyoming can be found in Daily (4, p. 40). A single specimen was found in Indiana, too. Since *Chara zeylanica* is more abundant in southern locations and since a lack of or irregularity in cortication seems to occur in the Characeae relative to adverse growing conditions, this form may be this kind of expression. Map 9 shows the location of the single collection in Wyoming.

Specimen seen: YELLOWSTONE NATIONAL PARK: Along the Bechler River at Three Rivers Junction. July 27, 1954. *Ross Skiver* (RM, BUT).

10. CHARA GLOBULARIS Thuill. Flor. Env. Paris, ed. 2, p. 472. 1799.

This species is described under the name of *C. fragilis* Desv. in Robinson (9, p. 279) and it is described and illustrated under the same name in Daily (3, p. 164, plate 4B). See Horn af Rantzien (6, p. 264, plate 13, figs. 1-7, p. 14, figs. 1-7, for oospores).

Distribution in Wyoming (Map 10) is in ponds and lakes at 4,500-6,400 ft. in northern Wyoming. Elsewhere this species is usually associated with ooze or finely divided soil in the substrate. The information about the Wyoming habitats where it is found suggests this condition there, too.

Specimens seen: CROOK COUNTY: Sundance. July 8, 1896. (Contains some *Nitella opaca*) *A. Nelson 2249b.* (RM, BUT). PARK COUNTY: Swampy Lake, Sunlight Basin north of Cody. 6,400 ft. Shallow water. July 21, 1955. *C. L. Porter 6793.* (RM, BUT). SUBLETTE COUNTY: Wind River Mountains, 18 mi. NNW of Pinedale and about 1.7 mi. NNW of outlet of Lower New Fork Lake, SE ¼, NW ¼, sec. 9, T. 36N, R 110W. In a kettle depression atop Wisconsin till. Bridger National Forest. Aug. 21, 1960, *Robert C. Bright* (BUT).

11. CHARA DELICATULA Ag. Syst. Alg., p. 130. Lund, 1824. (Non Desv.)

For descriptions see Robinson (9, p. 280) and descriptions and illustrations are given in Daily (3, p. 165, plate 4C), under the name *C. verrucosa.*

Distribution (Map 11) in Wyoming is in the clear water of quiet ponds and lakes, usually in isolated tufts, and often associated with tepid water from geysers or hot springs. The elevational range is 6,000-8,000 ft. It has been noted before that this species does not compete well with other aquatic plants and occurs in isolated spots.

Specimens seen: CARBON COUNTY: Long Lake, Medicine Bow Range. 8,000 ft. In 2 ft. of clear water, July 8, 1954. *C. L. Porter 6512* (RM, BUT). SUBLETTE COUNTY: Near Big Piney on the Quintal Ranch, 6,400 ft. Shallow water of reservoir lake. Aug. 12, 1958. *C. L. Porter & Marjorie W. Porter 7638* (contains some *Chara contraria*) (RM, BUT). YELLOWSTONE NATIONAL PARK: Nez Perces Creek, abundant in the warm water of the creek. July 30, 1899, *A. & E. Nelson 6238* (RM); Firehole River, south of Madison Junction. 6,800 ft., in 2 ft. of tepid water of flowing stream. Aug. 5, 1953. *C. L. Porter 6384*. (RM, BUT).

Included here is the specimen reported by Nelson (8) identified by T. F. Allen as *Chara fragilis* Desv., *Nelson 6238*.

LITERATURE CITED

1. Allen, G. O. An annotated key to the Nitelleae of North America, Bul. Torrey Bot. Club 81 (1):35-60. Lancaster, Pa., Jan., 1954.
2. Allen, T. F. Characeae of America 1:1-64, figs. 1-54. New York. 1888.
3. Daily, F. K. The Characeae of Nebraska. Butler Univ. Bot. Stud. 6:149-171. 5 pls. 1944.
4. ———. The Characeae of Indiana. Butler Univ. Bot. Stud. 11:5-49. 1953.
5. ——— and Walter Kiener. The Characeae of Nebraska—additions and changes. Butler Univ. Bot. Stud. 13(1):36-46. 1956.
6. Horn af Rantzien, Henning. Recent charophyte fructifications and their relationship to fossil charophyte gyrogonites. Arkiv. för Botanik. u. a. Kungl. Svenska Vetenskapakademien. Sr. 2, 4(7):165-332. 19 pls. Stockholm. 1959.
7. Nelson, Aven. First report on the flora of Wyoming. Univ. Wyo. Exp. Sta. Bul. 28, p. 202. May, 1896.
8. ———. The cryptogams of Wyoming. Tenth Ann. Rpt. Wyo. Exp. Sta., p. 7, 1900.
9. Robinson, C. B. The Chareae of North America. Bul. N. Y. Bot. Gard. 4(13): 244-308. June 25, 1906.
10. Wood, R. D. A review of the Genus *Nitella* (Characeae) of North America. Farlowia 3(3):331-398. 2 pls., July, 1948.

GLACIAL AND POST-GLACIAL CHAROPHYTES FROM NEW YORK AND INDIANA

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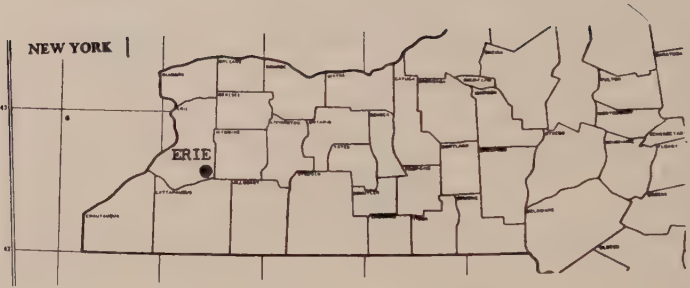
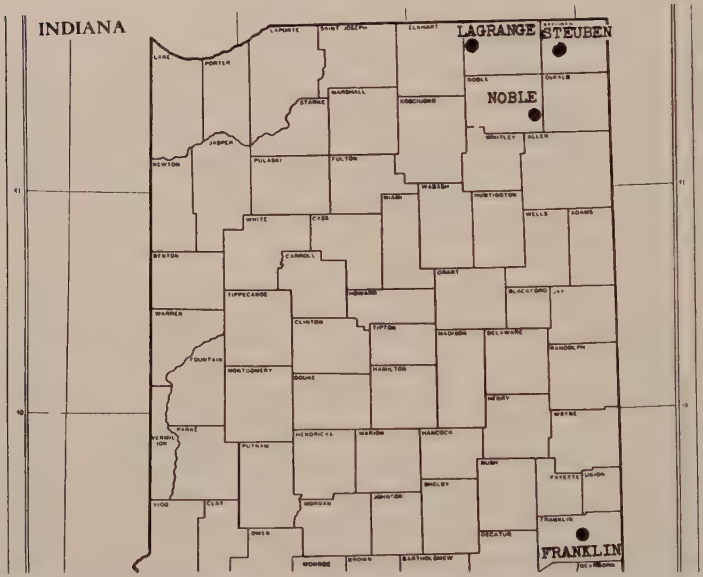
INTRODUCTION

Fossil charophytes from glacial and post-glacial deposits of North America have been studied very little, probably because they were expected to be similar to extant species for the most part and of little interest. The present study, however, disclosed charophytic remains of considerable variety, and extends chronologically the occurrence of several genera usually associated with older deposits.

COLLECTION DATA—GEOLOGY OF COLLECTION SITES

The specimens collected by W. J. Wayne came from several locations. The New York material is from a marl exposure along Nichols Creek, two miles south of Chaffee, Erie County (Arcade Quandrangle) (text-figure 1). Marl accumulated in a shallow depression in a pitted outwash plain that was deposited south of the Valley Heads Moraine when glacial meltwater escaped through Cattaraugus Creek. Nichols Creek now flows through the filled depression and has exposed the upper part of the marl. The lower part was sampled by coring until gravel was reached. The 0 to 1.1 foot level of the core sample is light yellowish gray marl containing wood fragments and mollusk shells. The charophytes isolated from it are *Charaxis, Charites strobilocarpa, Charites bitruncata, Latochara Waynei, Chara evoluta, Chara sejuncta, Chara contraria* and *Charites strobilocarpa* var. *ellipsoidea.* The 1.1 to 2.1 foot level is a medium to dark gray marl, lighter toward the base containing wood and shells. Fossil charophytes isolated from it are *Charaxis* , *Latochara Waynei, Charites strobilocarpa* var. *ellipsoidea, Grambastichara cylindrica, Obtusochara cylindrica, Charites bitruncata, Chara sejuncta* and *Chara evoluta.* The 2.1 to 2.9 foot level is white, sparsely fossiliferous marl containing *Charaxis, Charites strobilocarpa, Tolypella* sp., *Chara contraria, Chara evoluta, Charites strobilocarpa* var. *ellipsoidea, Charites bitruncata* and *Grambastichara cylindrica.*





Map of the western part of New York showing locations from which samples containing charophytes were collected.

Map of the northern and central parts of Indiana showing locations from which samples containing charophytes were collected.

Mollusks washed from the marl indicate that the sediment was deposited near the margin of a pond where it was heavily vegetated. Both pollen and snails suggest a climate that was somewhat cooler than the present. The site is also one from which part of the remains of a mastodon, now in the Buffalo Museum of Natural Sciences, was recovered. Wood from the base of the exposed marl at this locality has been dated by radiocarbon technique as 12,000 years old (Rubin and Alexander, 1960, p. 134, W-507).

It is interesting that a large number of *Chara contraria* oogonia and oospores were found in the early stage of this pond, as this species is an early inhabitant of gravel-bottomed ponds and lakes in present days. When the pond had matured, the most abundant species were *Charites strobilo-*

carpa var. *ellipsoidea, Chara sejuncta, Latochara Waynei* and *Charites bitruncata. Chara sejuncta* is typically from an aquatic habitat with mud or ooze bottom.

Specimens collected in Indiana came from several sites (text-figure 2). In Steuben County on the north side of Silver Lake, a marl digging exposed part of a former lake bed occupied by Silver Lake. This is located in the center NE¼ sec. 30, T. 37N., R. 13E. From the top down the deposit consisted of marl, interlayered with beds of peaty or mucky marl, 1.6 m. thick; marl, yellowish-white, granular, 0.9 m. exposed above water level. No sampling could be done below the water level even with a tube core sampler because the granular nature of the material and the high water content caused it to flow out of the tube. This particular sample (Field No. WJW-53-59B) is the lowermost of the two marl units exposed. It contained *Chara evoluta, Maedlerisphaeria ulmensis* and also 14 species of mollusks of which two, *Lymnaea parva* and *Gyraulus parvus* made up 83 per-cent of the sample. A small number of valves of *Pisidium* sp. were present; the remainder of the sample consisted of land pulmonates that inhabit vegetation around springs and marshy places. Both normal and zebrine forms of *Lymnea parva* and *Gyraulus parvus* were in the sample. The marl is post-Wisconsin in age.

In Lagrange County, Indiana, a core was taken along the southeast edge of Cass Lake, about 3 miles east of Middlebury, in the W½NW¼ sec. 5, T. 37N., R. 8E. (Field sample nos. WJW 53-64A and B). Cass Lake is in one of many depressions that formed in northern Indiana after the last glacier disappeared and probably came into existence when a buried ice block melted. Surrounding sediments are largely sand and gravel. Land drainage programs of the past few decades have lowered the water level in the lake and exposed some of the marl banks that were still accumulating at that time. The samples from which charophytes were collected came from the lower part of the following core: the 0 to 7.5 foot level consisted of light gray marl in which fossils were rare. The 7.5 to 10.5 foot level was of gray marl having very few fossils. In the 10.5 to 15 foot level was found gray, marly gyttja (Field sample no. WJW 53-64A) from which *Chara sejuncta* oospores were isolated. The 15.0 to 15.5 foot level was gray to black marly gyttja (Field sample no. WJW 53-64B) and contained *Charites bitruncata.*

Sediments in the lower part of this core were less calcareous than those in the upper part and contained a larger proportion of fine-grained organic debris. Mollusks were scarce throughout all of three cores taken from the south end of Cass Lake, thus ecologic interpretations based on mollusks species cannot be made. Presumably, however, the peaty marl and gyttja in the lower part of this core were deposited within the first few thousand years following deglaciation, while the dominant forest vegetation was coniferous trees and a somewhat cooler climate than the present prevailed.

In Noble County, Indiana, a peat bed was studied, located in a gravel pit in NW¼NE¼ sec. 13, T. 33N., R. 11E., along Little Cedar Creek (Garrett Quadrangle) (Field sample no. WJW 55-7). Since 1955, when the materials in this pit were studied, the gravel operation has destroyed most of the exposure. The section exposed in 1955 reported by Wayne and Thornbury (1955, p. 10) consisted of 6 feet of gravelly sand over 2 feet of highly fossiliferous marly muck that in turn overlay gravel. Till underlay the gravel at a depth of about 12 feet below the water in the pit. The dark gray marly muck sandwiched between two beds of sand and gravel contained abundant wood fragments, spruce cones, and mollusk shells. Wood from this bed has been dated as 12,300 years old (Suess, 1954, p. 470, W-58), thus the sediment represents early postglacial material in Indiana. Undoubtedly it represents the sediments deposited in a shallow basin or slough that existed in the valley train outwash along Little Cedar Creek, and the gravel and sand above the fossiliferous bed were laid down subsequently as channel or floodplain sediments. This sediment contained *Charites strobilocarpa* var. *ellipsoidea, Clavatorites noblensis, Charites bitruncata, Charites strobilocarpa* and *Chara evoluta.*

In Franklin County, Indiana, exposures along the bed and banks of Yellow Bank Creek reported by Wayne and Thornbury (1955, p. 27) were studied. The location is SW¼SW¼ sec. 34, T. 12N., R. 13E., 3 miles northwest of Brookville (Field sample no. WJW 58-16A). Tributaries of major glacial sluiceways such as the Whitewater Valley were ponded during each of the glaciations of the Pleistocene Epoch as a result of a gravel dam that accumulated at their mouths. Sediments exposed in Yellow Bank Creek record the events that affected the valley during the Wisconsin glaciation while ice approached the area. A massive, yellowish-gray, fossiliferous silt, the lowermost unit exposed, is overlain by non-fossiliferous, laminated, silty clay. Sand and till overlie the laminated sediments a short distance upstream and represent the sediments laid down as ice entered the valley from the north. The lake sediments increase in coarseness toward the mouth of the valley.

The massive, fossil-rich bed at the base of the exposed section contains wood, mosses, and mollusks. The upper 10- 20 cm. of the bed is contorted locally and contains a mollusk fauna dominated by small, cool water species, including *Gyraulus altissimus, Lymnaea parva,* and *Pisidium* sp. Charophytes found there are *Charaxis, Chara sejuncta, Latochara spherica* and *Latochara latitruncata.* The lower part of the same bed contains a similar fauna but includes the large *Lymnaea palustris* and *Oxyloma retusa* along with the smaller forms. All of these faunal species live in the moderate to heavy vegetation in shallow water and above the water on plants.

The entire unit probably was deposited in relatively shallow water that flooded the valley when glacial outwash gravels began to accumulate in the Whitewater Valley. Thus glacial ice probably was no farther than 50 or 60 miles to the north. Deposition of the overlying barren, laminated, silty clay took place when the dam of outwash gravel thickened with the approaching ice sheet and thus deepened the water in the lake.

METHODS

Collections were soaked in water containing a detergent until the particles separated. Some charophyte oospores floated and were removed from the top of the liquid. Then the sample was screened to separate remains of different sizes and allowed to dry. Charophyte oogonia, oospores and vegetative fragments were sorted from the screened sample by means of a damp camel hair brush while viewing under the microscope.

Fossils were not sectioned, but the preservation of the oospores inside the lime-shell facilitated determination of the thickness of the spirals (spiral cells). When wet, thin areas of the lime-shell appeared darker than thicker areas due to the dark oospore showing through. These observations could be verified when lime-shells were partially broken.

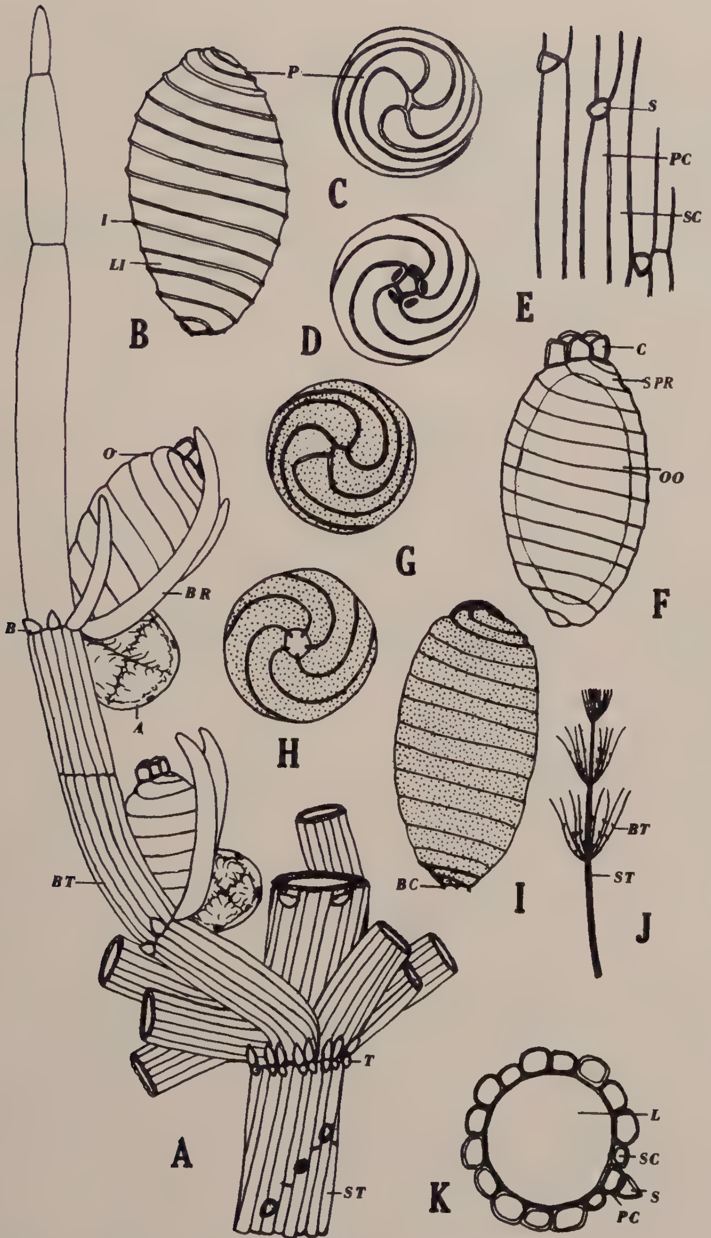
Photographs of the charophytes were taken by the author employing a Bausch and Lomb stereoscopic microscope with 15X ocular and 5.9X objective for most of the illustrations. A Model 800 Polaroid Land Camera was rested lens to miscroscope ocular with a distance of 3½ feet and 17 shutter control. Type 47, speed 3000 film was used. Glossy lime-shells were dulled by treating with dilute Shaeffer's writing fluid (blue black) number 22. Methylene blue can also be used. For reflected light, a 100 W. Bausch and Lomb Microscope Lamp was employed with diaphram nearly closed to provide about a ¾ inch opening affording a reduced light beam. Diaphram to specimen was about 8 inches. To backlight the specimens, a small glass reflector ⅛ by 1/16 inch with beveled edges on the reflecting face was used. The coated back was composed of two planes at a 45° angle to the two long edges of the reflector face meeting at a line at the center back, and two triangular planes at the same angle to the face on each side. The reflector, tipped slightly forward, was cemented to a cover glass and could be placed close to the back of the specimen facing the light. Before photographing, specimens were placed in a minute drop of water with a damp camel hair brush on a glass slide and manipulated into proper position on the glass stage using a black metal background. A few pictures were taken using a white background. Immediately upon drying, the picture was taken using a 5 second exposure.

Some pictures of the oospore membrane were taken with another microscope at a higher magnification, and a few illustrations of vegetative material and fruiting bodies were taken at a low magnification. Lateral views of lime-shells and oospores are arranged in the plates with the bases down and apices up or nearly so.

Charophytes are stored with the author's herbarium in small plastic boxes or Falcon plastic serological plates containing 10 wells each, sealed with glass cover slips. One cardboard slide with well completes the storage.

STRUCTURE OF A COMMON CHAROPHYTE

The plant form of modern charophytes is diverse, but fundamentally consists of a *stem* branched or unbranched with nodes and internodes. At the nodes are whorls of *branchlets* greatly differing in organization in different genera of the Characeae. Text-figure 3 shows *Chara contraria* A. Br. ex Kütz. This species grows as a condensed form in shallow water or may be several feet long in deep water. In J, the tip of the plant is seen to be composed of a stem bearing four whorls of branchlets, each whorl having about eight branchlets. A illustrates an enlarged view of a stem node with one branchlet shown in detail. The short section of stem shown above and below the node appears striated. The internodal portion of the stem consists of a very large central cell extending from node to node along the stem axis covered externally by a layer of cells, one cell thick, called the *cortex* which produces the striated appearance of the stem. One of the chief distinguishing characteristics used in the Characeae is the presence or absence of cortex and its nature if present. In the stem of *Chara contraria* there are prominent *primary cortex* cells distinguished by having nodes and internodes with one-celled *spines* produced at the nodes. *Secondary cortex* cells do not have the nodal-internodal alternation and produce no spines. They are less prominent than the primary cells in *Chara contraria.* (The longitudinal strip of cortex in E and the stem cross section in K show the details of structure in a more enlarged view.) At the bases of the branchlets in A, it is seen that there are two circles, one above the other around the stem, of one-celled processes termed *stipulodes.* The branchlet illustrated in detail is unbranched, possessing two corticated internodes at the base and a 3-celled undifferentiated ecorticate tip. At the two nodes are whorls of 1-celled processes. The long ones associated with the gametangia are termed *bracteoles,* the posterior short ones are *bracts.* An *oogonium* and an *antheridium* below it are produced at the nodes of the branchlets in this monoecious species. The term *oogonium* is used here as it is commonly employed in reference to the Characeae to indicate the many-celled reproductive organ including besides other sterile cells and the egg cell, the *spirals* or spiral cells topped by the



The structure of *Chara contraria* Braun ex Kützing
a, antheridium; b, bract cell; bc, basal claw; br, bracteole; bt, branchlet; c, coronula; i, intercellular ridge; l, central cell lumen; li, lime-shell; o, oogonium; oo, oospore; p, peripheral groove; pc, primary cortex cell; s, spine cell; sc, secondary cortex cell; spr, spiral cell; st, stem; t, stipulode. A, Stem node with one branchlet shown in detail. B-D. Lime-shell of a mature oogonium shown in lateral, apical and basal views respectively. E. Portion of stem cortex in external surface view. F. Oogonium after fertilization previous to heavy deposition of lime. G-I. Oospore divested of outer spiral covering (lime-shell) in apical, basal and lateral views, respectively. J, Apical portion of plant, natural size. K. Cross section of stem.

coronula. The coronula may be 5-celled as in *Chara contraria* or another tier of five cells may be produced to form a 10-celled coronula in other genera. The term *oogonium* is commonly applied to the complex female reproductive structure after fertilization of the egg, also, because the exact time of fertilization cannot be determined satisfactorily by casual observation. Several changes take place upon maturation of the fertilized egg to form the *oospore.* It becomes covered with an outer and inner *colored membrane* (the sporostine and ectosporine respectively of Horn af Rantzein, 1959b, p. 197) and an outer and inner colorless membrane (the *endosporine* of Horn af Rantzien, 1959b, p. 197). Starch grains and oil droplets are stored inside the oospore.

The term *antheridium* is also used here as it is commonly applied in the Characeae to designate the globular body consisting of the covering of *shield cells,* enclosed sterile cells, and the *antheridial filaments* made up of the cells giving rise directly to the male gametes.

The terms *antheridium* and *oogonium* are considered inappropriately used in this way by some authors who restrict the use of the terms to the enclosed single cells which directly produce gametes. Unfortunately, the terms proposed to replace them usually have been applied in another connotation in the algae or higher plants or have become associated as synonymous with the terms which they are to replace and so are subject to the same inappropriateness and confusion.

Some authors also think that *oospore* should be confined to indicate the structure enclosed by membrances directly derived from the fertilized egg rather than include the complete membranous covering of the fruiting body including the outer colored membrane which may be derived from the spiral cells. *Oospore* is used in this paper to indicate the fruiting body enclosed by the outer colored membrane.

If considerable resistance is present toward the terms *oogonium* and *oospore,* as used commonly in the charophytes, perhaps they could be replaced by the following: *gyrogonium-* many-celled female reproductive organ in the charophytes (unfertilized or oospore producing, covered externally by the outer spiral cell walls; or if a lime-shell is produced and the outer integument disappears, the outer covering would be the lime-shell; or, in some instances, a utricle might be produced to partially or totally cover the exterior of the organ); *gyrospore-* a structure produced after fertilization of the egg, covered externally by the outer colored membrane. A term for this latter structure seems desirable since it is a natural unit, easily isolated in extant and some fossil charophytes. A valuable taxonomic tool is provided by its characteristics, some of which could be ascertained in sectioned fossil material and compared with isolates. If these terms were adopted, it is hoped that they be only defined in glossaries and not cited in synonomy with other terms subject to confusion.

The derivation of the proposed terms is from Greek. *Gyrogonium* is from the combining forms *gyro,* spiral, referring to the covering of spiral cells or derivatives, and *gonium,* reproducing cell. *Gyrospore* comes from the combining forms *gyro* and *spora,* seed. These appellations are seen to have parts in common with the familiar, *gyrogonite,* used to designate fossil charophytic fructifications. It seems that *gyrogonium* and *gyrospore* might be suitable to indicate both extant and fossil structures; but if not, *gyrogonite* could be used to indicate a fossil *gyrogonium* and *gyrosporite* for a fossil *gyrospore.*

Text-figure 3F shows an oogonium of *Chara contraria.* It is covered by five *spiral cells* which spiral to the left around the organ producing the striae at their lateral walls and are topped by a crown of five cells called the *coronula.* The distal end of the oogonium and oospore is called the *apical pole* and the proximal is the *basal pole.* Measurements are taken of the widest part across fructifications and from the apex to the base along the longitudinal axis. The ends of the spiral cells as they approach the apex may be modified in various ways to produce useful systematic characteristics, and the width of the spirals at the basal pole is compared with the width at the equator. The typical configuration of the spiral cell ends at the apex of the oogonium of *Chara contraria* is seen in C and at the base in D, and the apex and base of the oospore are in G and H. In H, it can be seen that the *basal claws* are clasping the white calcified *basal plug* which is pentagonal in basal view. It is filling the depression outlined by the pentagonal base of the oospore. During maturation of the oospore in *Chara contraria,* lime is deposited within the spiral cells of the oogonium, so that a *lime-shell* (B) is formed covering the oospore. Some species do not produce a lime-shell. At the lateral junction of the spiral cell walls of the lime-shell in B, the low *intercellular ridges* are formed. At the periphery of the apical pole (B and C) of the lime-shell, a groove is formed by the decrease in width and thickness and increase in concavity of the spiral cells. They then expand to meet along an irregular line at the apex. At the basal pole of the lime-shell (D), the spirals meet at the pentagonal base. In *Chara contraria,* a pore is found at the center of the basal pole partly filled by the thin basal plug. Perforations in the spirals around the basal opening are also found in this species.

For structure, development and a glossary of terms for the charophytes, the work of Groves and Bullock-Webster (1920, p. 16-76) is recommended. Terms used here have been selected chiefly from that publication and Horn af Rantzien (1956, p. 212-259).

NATURE OF FOSSIL CHAROPHYTE REMAINS

Lime-shells (mature and immature), oospores and calcareous stem and branchlet fragments were preserved. In some genera of fossil charophytes, a covering is developed over the lime-shell, called the *utricle,* but none were found in the specimens reported here. Coronulas were not preserved and so not found in any of these specimens, either. Lime-shells were, for the most part, easily cleaned of debris with needles and brush, but a few were split and delicate requiring a minimum of handling. Bits of outer spiral cell wall or *integument* were occasionally found adhering. In one instance, (*Obtusochara cylindrica*) an immature lime-shell was particulate in nature and organic remains of the spiral cells were still pliable and could be unwound to produce the five spiral units.

Many oospores were found, some divested of lime-shells or partly so, and some were isolated from the lime-shells when ample material was available. The oospores appeared to have only the outer and inner colored membranes preserved, but although the contents had disappeared, they retained their original shape with only small areas collapsed for the most part. Slight mineral deposits were found in some.

The vegetative material was fragmentary and difficult to examine because of mineral deposits on the exterior of the stems, particularly.

ACKNOWLEDGEMENTS

The author is grateful for: the encouragement given by W. A. Daily; the samples, geological interpretations and ecological data based on mollusks provided by W. J. Wayne; the grant to help finance the photography given by the A.A.A.S. through the Indiana Academy of Science Research Foundation Committee; slides for the paper presented at a meeting of the American Institute for Biological Sciences provided by Eli Lilly and Company; copies of the photographs providing negatives by Eli Lilly and Company; photocopies of several articles supplied by Eli Lilly and Company and Indiana University; and the aid in making inter-library loans by the Butler University Library.

SYSTEMATIC SECTION

Considerable difference of opinion has been expressed about classification of isolated fossil organs assigned to the charophytes. Proponents of strict adherence to referring all isolated fossil fruiting bodies to artificial taxa within this division, readily refer these structures, however, to the charophytes, even though major divisions in the algae are differentiated, primarily, on the basis of pigments. The above classification is obviously based on morphology of a plant part. It seems logical, then, to extend this policy to lower taxa, too. Therefore, the unattached fossil charophyte organs reported here are referred to taxa for extant charophytes when the morphological characteristics preserved are similar, and to organ species and genera when similar unattached organs are known only from the fossil record.

KEY

The following key to the genera of charophytes is based on characteristics of the lime-shell; all lack a utricle and have 5 (4-6) spiral cells:

Apical pole bearing a cylindrical projection (neck) formed by upturned ends of spiral cells surrounding a small opening at apex.
  Groove absent at apical periphery .... 1. *Clavatorites*
Apical pole ± conical, subtruncate or rounded to protruding Groove at the periphery of the apical pole
  Spirals wider at base than at equator .... 2. *Charites*
  Spirals more or less the same width at base as at equator .... 3. *Chara*
Apical pole broadly truncate
  Groove at periphery of apical pole, conical projection at apical center........................ 4. *Latochara*
    Groove absent at periphery of apical pole. Prominence or depression absent at apical center .... 5. *Obtusochara*
Apical pole bearing a rosette or apical cap formed by the marked expansion of spiral cell ends. Groove at apical periphery
    Spirals form indistinct depressions in apical periphery .... 6. *Maedlerisphaera*
    Spirals lack depressions in apical periphery... 7. *Grambastichara*

In addition to those charophytes keyed, one oospore is referred to the genus *Tolypella* and all vegetative remains are classified as *Charaxis*.

DESCRIPTIONS

Division CHLOROPHYTA
Class CHAROPHYCEAE
Order CHARALES
Family CLAVATORACEAE

1. Organ-genus CLAVATORITES Horn af Rantzien, 1954

Clavatorites noblensis Daily, new species

Lime-shell without utricle and developed by 5 spiral cells, 827 μ long (neck included which is 175 μ long) 470 μ broad, ellipsoid-elongate, tapering at the summit to form a neck, narrowly truncate at the base, 13 inconspicuous ridges in lateral view. Lime-spirals 5, thin, nearly flat except at base and apex where they are somewhat concave, not forming a groove at the apical periphery, turning upward at the summit to form a cylindrical projection (neck) with little change in diameter, meeting at the apical center around a narrow opening, turning out to form a small, 5-lobed lip, widening at the base to meet at a large pentagonal depression which is outlined by black organic remains presumably extending from the base of the oospore through the lime-shell. Surface of the lime-shell yellowish-white, smooth, glossy and punctate in reflected light.

Oospore dark brown, dull, ellipsoid-elongate, 745 μ long, 450 μ wide, tapering to base and apex, apex conical and protruding, base narrowly truncate, 11 prominent ridges in lateral view. Spirals approach base and apex with little change in diameter, turn upward at apical center to meet around a small opening. This description is based upon some unique oospores broken from their lime-shells, which because of their shape, size, strong ridges, apical opening and association in the same collection as well as the unique apical structure are tenatively assigned to this species until more oogonia of *Clavatorites noblensis* can be found in order to isolate oospores substantiating or refuting this assumption.

This species differs from *Clavatorites höllvicensis* Horn af Rantzien (1954, p. 48), to which it seems most closely related, chiefly in having a long neck at the apical center and its larger size. The neck and spiral endings at the summit are similar to *Clavator harrisi* Peck (1941, p. 292), but it differs from that species in several respects, particularly, in lacking a utricle. In lateral view, it is somewhat similar to some species assigned to *Stellatochara* by Horn af Rantzien (1954, p. 26), but does not have a stellate apical opening, is more elongate, and has a longer, narrower neck.

Specimens Seen: *Illustrated:* oospore (Plate 5, fig. 12, right), Slide 4-4, oospore (Plate 5, fig. 14), Slide 4-4, Noble Co., Ind.; oogonium (HOLOTYPE), (Plate 5, figs. 15-17), Slide 4-1, Noble Co., Ind. *Not Illustrated:* 5 oospores, Slide 4-4, Noble Co., Ind. (Slide 1-1, etc. = serological plate 1, well 1, etc.)

Family CHARACEAE

2. Organ-genus CHARITES Horn af Rantzien, 1959 a

Charites bitruncata (Reid and Groves) Horn af Rantzien

Chara strobilocarpa var. *bitruncata* REID and GROVES, 1921, Quart. Jour. Geol. Soc. of London, pt. 3, no. 307, p. 188, pl. V, fig. 13.

Charites bitruncata (Reid and Groves) HORN AF RANTZIEN, 1959 a, Acta Univ. Stockholm., Stockholm Contrib. in Geol., vol. 4, no. 2, p. 67, pl. III, figs. 1-4.

Lime-shell without utricle and developed by 5 spiral cells, ellipsoidal, apical pole rounded to subtruncate, base rounded to slightly protruding, showing 11-12 prominent intercellular ridges in lateral view, 720-750 μ long, 500-535 μ wide. Spirals concave, narrowed at the apical periphery, then widened again before meeting in a zigzag line at the apex. Spirals widening at the basal pole before they meet at the pentagonal base which is 88 μ broad.

Oospore ellipsoid-elongate, tapered to base and summit, 635-685 μ long, (including the peak which is 30 μ long and the basal claws which are 50 μ long), 350-385 μ wide, brown (probably immature) to shiny black, showing 11 striae in lateral view. Spirals slightly concave, narrow in apical periphery then widen on the apical pole to meet at the apical center in a peak, widen somewhat approaching base. Surface punctate in reflected light. Basal plug pentagonal in basal view (Plate V, fig. 7) 105 μ across the base, 125 μ across the top, and 50 μ thick (Plate 4, fig. 5), apparently convex and thinner at center based on study with transmitted light.

This oospore differs from that of *Chara globularis* Thuill. which it superficially resembles, in its strong peak at the summit, larger angle of the spirals at the equator, strongly tapering summit and base, widening of spirals as they approach the base, and the size.

Previous Occurrence. Lower Headon Beds, Hordle (Hordwell) Cliffs (South Hampshire), England, Upper Bartonian, Eocene.

Specimens Seen: *Illustrated:* Oospore (Plate 2, fig. 9), Slide 1-6, 1.1-2.1 ft. level of core, Erie Co., N. Y.; oogonium and oospore isolated from it, (Plate 4, figs. 4-7), Slide 2-2, oogonium, (Plate 4, figs. 14-16), Slide 2-10, 0-1.1 ft. level of core, Erie Co., N. Y.; oospore (Plate 5, figs. 7-9), Slide 5-2, LaGrange Co., Ind. *Not Illustrated:* 10 oospores, Slide 5-7, 12 oospores, Slide 5-8, 0-1.1 ft. level of core, Erie Co., N. Y.; oospore, Slide 3A-1, 2 oospores, Slide 3A-2, 5 oospores, Slide 3A-4, 2.1-2.9 ft. level of core, Erie Co., N. Y.; ca. 30 oospores, Slide 4-2, ca. 30 oospores, Slide 4-3 & 4, Noble Co., Ind.

Charites strobilocarpa (Reid and Groves) Horn af Rantzien

Chara strobilocarpa REID and GROVES, 1921, Quart. Jour. Geol. Soc. of London, vol. 77, pt. 3, no. 307, p. 187, pl. V, figs. 7-8.

Charites strobilocarpa (Reid and Groves) HORN AF RANTZIEN 1959 a, Acta Univ. Stockholm., Stockholm Contrib. in Geol., vol. 4, no. 2, p. 61, pl. II, figs. 4-8.

Lime-shell without utricle and developed by 5 spiral cells, elongate-ellipsoidal, 870 μ long, 500 μ wide, apical pole and base protruding and subtruncate. Lime spirals very concave, showing 11 prominent intercellular ridges in lateral view, 75 μ in diameter at the equator of the oogonium, becoming 145 μ wide near the apical center and base, narrowing at the apical periphery before widening and turning onto the apical pole, meeting at the apical center along a short line, producing very prominent intercellular ridges at the base where they meet at the pentagonal depression which is 75 μ in diameter. Lime-shell 55 μ thick at equator, creamy white, surface glossy and punctate in reflected light.

Oospore black, glossy, 750-800 μ long, 370-420 μ wide (including peak and cage), elongate-ellipsoid, tapering somewhat to base and apex. Apex narrowly truncate with spirals upturned. Base producing a cage, 135 μ long, containing a calcareous plug, 135 μ across the top and 110 μ across the bottom and 70 μ thick. Spirals forming a peak 105 μ long at the apex, narrowing at the periphery of the apical pole, widening as they turn upward to meet at a point on the summit. Surface of oospore punctate in reflected light.

Previous Occurrence. "Limestone band", Lower Headon Beds, Hordle (Hordwell) Cliffs (South Hampshire), England, Upper Bartonian, Eocene.

Specimens Seen: *Illustrated:* oogonium, (Plate 1, figs. 7-9), and oospore isolated from it (Plate 1, figs. 4-6), Slide 3-2, 2.1-2.9 ft. level of core, Erie Co., N. Y.; oospore, (Plate 5, fig. 13), Slide 4-4, Noble Co., Ind. *Not Illustrated:* 3 oogonia and 2 oospores, Slide 5-7, oogonium, Slide 2A-3, 0-1.1 ft. level of core, Erie Co., N. Y.; oospore in each of Slide 3-8, Slide 3A-1, Slide 3A-2 and Slide 3A-4, 1 oogonium, Slide 3A-3, 2.1-2.9 ft. level of core, Erie Co., N. Y.; 15 oospores, Slide 4-2 to 4, Noble Co., Ind.

Charites strobilocarpa var. **ellipsoidea** (Reid and Groves) Daily, new combination

Chara strobilocarpa var. *ellipsoidea* REID and GROVES, 1921, Quart. Jour. Geol. Soc. of London, vol. 77, pt. 3, no. 307, p. 188, pl. V, fig. 10.

Dr. Horn af Rantzien examined specimens of *Chara strobilocarpa* and *Chara strobilocarpa* var. *bitruncata* when these were transferred to the Genus *Charites*. However, he (1959 a, p. 63) states, "No specimens have been examined and neither from the description nor from the illustration (Reid and Groves, op. cit., pl. V, fig. 10) can it be decided whether the var. *ellipsoidea* is conspecific with *C. strobilocarpa* or not."

Since the specimens reported here seem to fit the illustration and description of *Chara strobilocarpa* var. *ellipsoidea* very well, were found associated with *(Chara) Charites strobilocarpa* and appear to be conspecific with it, it seems desirable to retain this variety. Since *Chara strobilocarpa* has been transferred to *Charites,* it is necessary to make a new combination for the var. *ellipsoidea.* In the absence of typification, Plate V, fig. 10, (Reid and Groves, op. cit.), is designated as the lectotype.

Their description is interpreted to establish the variety as differing from the type chiefly by the oogonium being somewhat tapered at both ends, slightly more below than above or ellipsoid as the name and illustration indicate, rather than protruding at the base and summit as is typical.

Lime-shell without utricle, developed by 5 (4-6) spiral cells, elongate-ellipsoid, slightly pointed at base and apex or base slightly truncate, 620-785 μ in length (including slight peak) 450-500 μ in width, 11-12 ridges in lateral view (variant, 4-spiralled oogonium 620 μ long, 450 μ wide having 9 ridges in lateral view). Spirals not quite as strongly concave as in type (only slightly concave in 4-spiralled oogonium), narrowing slightly at summit periphery and then widening considerably before meeting on the apical pole along a short line, widening also at the basal pole before meeting at the pentagonal (4-6-sided) base which is 120 μ wide (70 μ in 4-spiralled oogonium). Ridges prominent at base and summit. Lime-shell thin, smooth, off-white, glossy, surface punctate in reflected light.

Oospore dark brown (almost black), elongate-ellipsoid, tapering slightly at apex to a short peak similar to, but shorter than the type, base narrowly truncate with prominent ridges extending to form short claws, less than 620-735 μ long (including peak), 350-370 μ wide, 12 striae in lateral view. Spirals narrow at the apical periphery, widen before turning upward to form peak, widen somewhat before meeting at pentagonal (4-6-sided) base. Membrane punctate in reflected light.

Previous Occurrence. "Limestone band." Lower Headon Beds, Hordle (Hordwell) Cliffs (South Hampshire), England, Upper Bartonian, Eocene.

Specimens Seen: *Illustrated:* Variant, 4-spiralled oospore, (Plate 1, figs. 15-17), Slide 3-9, 2.1-2.9 ft. level of core, Erie Co., N. Y.; variant, 4-spiralled oogonium, (Plate 3, figs. 1-3), lost, 5-spiralled oogonium (Plate 3, figs. 10-12), Slide 1-4, a variant 6-spiralled oogonium, (Plate 3, figs. 16-18, Slide 1-1, 1.1-2.1 ft. level of core, Erie Co., N. Y.; 5-spiralled oogonium, (Plate 4, figs. 17-19), Slide 2A-1, 0-1.1 ft. level of core, Erie Co., N. Y.; oospore (Plate 5, fig. 12 on left, Slide 4-4, Noble Co., Ind. *Not Illustrated:* 15 oospores, Slide 1A-1, and oospore isolated from an oogonium, Slide 1A-6, 10 oogonia, Slide 1-7, 1.1-2.1 ft. level of core, Erie Co., N. Y.; 6 oospores, Slide 3A-4, 5 oospores, Slide 3A-5, 2.1-2.9 ft. level of core, Erie Co., N. Y.; 30 oospores and an oogonium, Slide 4-3 & 4, Noble Co., Ind.

3. Genus CHARA Linnaeus, 1753

Chara evoluta T. F. Allen

Chara evoluta T. F. ALLEN, 1882, Torrey Bot. Club, Bull., vol. 9, no. 4, p. 41, pl. 19.

Lime-shells absent.

Oospore ellipsoid-oblate, apex and base broadly rounded or only slightly tapering, 10 inconspicuous striae in lateral view, 460-650 μ long, 300-405 μ wide, dark brown, dull, surface punctate in reflected light. Spirals narrow slightly in apical periphery, then widen to meet along a short line at apical center, little change in width at basal pole where they meet at a pentagonal depression 88 μ in diameter. Outer colored membrane brown, granulate in transmitted light.

Previous Occurrence. Although a somewhat similar brackish water species, *Chara canescens,* has been found in the fossil state, the brackish and fresh-water *Chara evoluta* apparently has been known only from recent collections, exclusively, and is found in widely scattered areas in North America. The type locality is Saskatchewan, Alberta, Canada, in lakes and ponds. It has also been reported from ponds and lakes in Nebraska (Daily, 1944, p. 158), from Little Compton, Rhode Island by Wood (1949, p. 197), and from lakes and ponds in British Columbia (Allen, 1951, p. 151). It has also been found in mineral springs at 7000 ft. elevation in Colorado (collector unknown).

Specimens Seen: *Illustrated:* Oospore (Plate 1, figs. 22-24), Slide 3-4, oospore (Plate 1, figs. 28-30), Slide 3-1, 2.1-2.9 ft. level of core, Erie Co., N. Y.; oospore (Plate 2, figs. 26-28), Slide 1A-4, 1.1-2.1 ft. level of core. Erie Co., N. Y.; oospore, (Plate 5, figs. 4-6 and outer colored membrane, Plate 5, fig. 10), Steuben Co., Ind. *Not Illustrated:* Oospore, Slide 2-8, 0-1.1 ft. level of core, Erie Co., N. Y.; 25 oospores, Slide 6-2, Steuben Co. Ind., 12 oospores, Slide 4-4, Noble Co., Ind.

Chara contraria Braun ex Kützing

Chara contraria BRAUN ex KÜTZING, 1845, Phyc. Germ., p. 258.

Lime-shell without utricle, developed by 5 spiral cells, ellipsoid-prolate, top broken so complete fossil unknown, base narrowly truncate and protruding. Spirals slightly concave, almost flat, ridges moderately prominent, strongly developed at the pentagonal base which is 85 μ in diameter. Lime-shell grayish-white, surface punctate in reflected light.

Oospore sooty brown, surface punctate in reflected light, ellipsoid-prolate, 12-14 prominent striae in lateral view, base narrowly truncate and protruding, summit protruding, ca. 650 μ long, 320 μ wide. Spirals narrow at the periphery of the summit then expand to meet at the apex in a short irregular line, turn onto the basal region without much change in width and meet at a small pentagonal depression. The basal plug is retained in the basal depression in the view shown in Plate 1, fig. 20, but is removed in Plate 1, fig. 21.

Previous Occurrence. This species has been reported from the Quaternary of Europe several times, but this is the first fossil record for North America as far as is known. A recent species, it grows in a rather wide range of habitats, but is conspicuous as the early inhabitant of gravel pit ponds in Indiana, and elsewhere. It has been reported several times for New York (Wood & Muenscher, 1956, p. 36) and Indiana (Daily, 1953, p. 43).

Specimens Seen: *Illustrated:* broken oogonium showing top of oospore, (Plate 1, figs. 11-13), and oospore isolated from it, (Plate 1, figs. 19-21), Slide 3-3, oospore, (Plate 2, figs. 6-8), Slide 3-7, 2.1-2.9 ft. level of core, Erie Co., N. Y. *Not Illustrated:* 3 oospores, Slide 5-6, 0-1.1 ft. level of core, Erie Co., N. Y.; 16 oospores, Slide 3A-1, 11 oospores, Slide 3A-2, 20 oospores, Slide 3A-4, 45 oospores, Slide 3A-5, 2.1-2.9 ft. level, Erie Co., N. Y.

Chara sejuncta Braun

Chara sejuncta BRAUN, 1845, Boston Jour. Nat. Hist., vol. 5, p. 264.

Lime-shell without utricle and developed by 5 spirals, prolate-ellipsoid, or subovoidal, 750-785 μ long, 450-500 μ wide, 12 or 13 inconspicuous striae in lateral view, summit slightly protruding and broadly rounded, base protruding and truncate. Lime spirals thin, slightly concave, narrow in apical periphery, then expand to meet along a short line at the apex, approach the base without much change in diameter until the ends, which narrow and project slightly around the pentagonal depression at the base. Base 75 μ in diameter. Immature lime-shell thin, rough, dull (Plate 5, figs. 18-20). Mature lime-shell smooth, glossy, off-white, punctate in reflected light (Plate 3, figs. 19-21).

Oospore dull, dark brown, ellipsoid-elongate, apical pole and base protruding and narrowly truncate, 685 μ long, 350 μ wide, 12 striae in lateral view which are inconspicuous except at summit where they form a crest and at the base where they form claws. Spirals narrow in apical periphery where a groove is formed, expand to meet along a short line at apex, not much wider at the pentagonal depression at the base which is 90 μ in diameter. Basal plug thin (Plate 4, fig. 3). Surface of oospore punctate in reflected light.

Previous Occurrence. Apparently the only fossil record of this species is by Horn af Rantzien (1951, p. 666) as follows: "Pleistocene, at the eastern end of Lake Tacarigua (= L. Maracay), northern Venezuela. – –" The type locality of this recent species is in lakes in the lowlands of the Mississippi, Illinois, opposite St. Louis, Missouri. Robinson (1906, p. 297) gives the distribution as, "Massachusetts and Alabama to Minnesota and Mexico; also reported from South America." Horn af Rantzien (1950, p. 398) gives the distribution for Latin America as: Mexico, West Indies, and in South America–Brazil, Colombia, and Bolivia. It has been reported by Prescott (1951, p. 340) for Wisconsin and by Wood and Muenscher (1956, p. 36) for New York. In Daily (1953, p. 43-44), it can be seen that this species has been collected in many types of habitats in Indiana including ponds (artificial, sink-hole, seepage, stream fed), rivers, lakes of glacial origin with collected mud or muck on the bottom (stream fed), and strip mine ponds. The chief factors in common, though, seemed to be the mud, muck or ooze bottom of the body of water, and that the species is more abundant in southern localities, although it is occasionally found in the northern part of the state.

Specimens Seen: *Illustrated:* Oogonium (Plate 3, figs. 19-21) and the oospore isolated from it (Plate 4, figs. 1-3), Slide 1-10, 1.1-2.1 ft. level of core, Erie Co., N. Y.; immature oogonium, (Plate 5, figs. 18-20), Slide 6-1, Franklin Co., Ind. *Not Illustrated:* 5 oospores, Slide 1A-2, 1.1-2.1 ft. level of core, Erie Co., N. Y.; 11 oospores, Slide 5-1, LaGrange Co., Ind.; crushed oospores and broken oogonia, Slide 6-1 and Slide 7, Franklin Co., Ind.; 5 oospores, Slide 5-8, 0-1.1 ft. level of core, Erie Co., N. Y.

4. Organ-genus LATOCHARA Mädler, 1955

Latochara Waynei Daily, new species

Lime-shell without utricle and developed by 5 spirals, 785-820 μ long (including peak), 500-550 μ wide, with 10-11 ridges in lateral view which are prominent and decorated with small projections, spheroidal or ovoid, basal pole rounded or somewhat tapering to the narrowly truncate base, summit broadly truncate with a conical projection or peak. Spirals usually decorated with small to large, rounded, low projections. Spirals slightly to moderately concave, narrow and more concave at the periphery of the summit, somewhat wider as they turn upward to form the conical projection at the apical center, narrowing gradually to a point at the apex where they surround a small opening. Some apical spiral ends are distorted to form a scroll (Plate 2, fig. 11) or are separated to form points. Spirals approach the base with little change in width where they meet at a pentagonal depression about 80 μ wide. Lime-shell surface moderately glossy, off-white.

Oospore 585-750 μ long, 370-420 μ wide, with 11 prominent ridges in lateral view, black, glossy, ovoid, rounded at base, truncate at summit which has a prominent peak (peak included in measurement of length). Spirals separated by very prominent ridges at summit, slightly concave, more concave in apical periphery where they narrow then widen to turn upward tapering to a point at the apex forming the peak, approach the pentagonal base (110 μ wide) with little change in width, outer colored membrane punctate in transmitted light (Plate 2, fig. 23 inset).

This species probably resembles *Latochara latitruncata* in shape more than any other species of the genus, but is larger and has decorated spirals of the lime-shell and the intercellular ridges are decorated. It is similar to *Latochara collina* in having decorated ridges, but differs in size, number of ridges and particularly in having the spirals also decorated, although decoration in *Latochara Waynei* is sometimes slight and variable in different parts of the same specimen.

Specimens Seen: *Illustrated:* oogonium, (Plate 2, figs. 11-13), (HOLOTYPE), Slide 1-5, oogonium, (Plate 2, figs. 20-22), oospore isolated from oogonium just cited (Plate 2, figs. 23-25) sacrificed for membrane illustrated (Plate 2, fig. 23 inset), Slide 7M, 1.1-2.1 ft. level of core, Erie Co., N. Y.; oogonium, (Plate 4, figs. 8-10), sacrificed for the oospore (not shown) Slide 2-3, 0-1.1 ft. level of core, Erie Co., N. Y. *Not Illustrated:* 3 oogonia, Slide 1-7, 3 oogonia, Slide 1-8, 1.1-2.1 ft. level of core, Erie Co., N. Y.; oogonium, Slide 2-7, broken oogonium, Slide 2A-4, 2 oogonia, Slide 5-7, 2 oogonia, Slide 5-8, 0-1.1 ft. level of core, Erie Co., N. Y.

Latochara latitruncata (Peck) Mädler

Aclistochara latitruncata PECK, 1937, Jour. Pal., vol. 11, p. 89, pl. 14, figs. 1-4.

Latochara latitruncata (Peck) MÄDLER, 1955, Geol. Jahrb., vol. 70, p. 271.

Lime-shell without utricle and developed by 5 spirals, slightly prolate spheroidal to top-shaped with broadly truncate apical pole which forms a low conical peak at the center, rounded to narrowly truncate at the base, 420-585 μ long (including peak, 335-420 μ wide, 9-11 striae—inconspicuous to prominent in lateral view. Spirals slightly convex or concave, concave in apical periphery where they are easily broken; turning upward on the summit to form a low, conical peak; widen as they turn upward, then narrow to a point at a small apical opening; meeting at the irregularly pentagonal base which is 80 μ in diameter without flanges or raised border. Lime-shell glossy, yellowish-gray, surface punctate in reflected light.

Oospore black, glossy, ovoidal, with a peak at the summit and truncate at the base, 370 μ long, 285 μ wide, with 9 low, intercellular ridges. Spirals narrow at apical periphery, then widen and turn upward narrowing again to a point forming a short peak, meet with little change in width at the basal depression.

Previous Occurrence. (From Peck, 1957, p. 33) "Brushy Basin shale member of the Morrison in east-central Utah (USGS paleobotanical locality D290) and in the undivided Morrison of central and eastern Wyoming and central Montana." Ross (1960, p. 720) reports this species from the Morrison of Colorado. All of these occurrences are Upper Jurassic, Mesozoic.

Specimens Seen: *Illustrated:* oogonium, (Plate 5, figs. 24-26), Slide 6-1, Franklin Co., Ind. *Not Illustrated:* 2 oogonia, (broken but identifiable), 2 oospores, Slide 6-1, Franklin Co., Ind.

Latochara spherica Peck

Latochara spherica PECK, 1957, U. S. Geol. Survey Prof. paper 294-A, p. 33, pl. 5, figs. 34-36.

Lime-shell without utricle and developed by 5 spirals, spheroidal, narrowly truncate summit area bearing a low conical peak, basal pole rounded but having a slightly truncate protrusion at the pentagonal base, 585-665 μ long (peak included, 501-535 μ wide, 10 or 11 prominent ridges (inclusion of short ridges at base and apex results in a larger number than is sometimes stated by other authors). Spirals concave, slightly more concave in apical periphery, then widen slightly as they turn upward to meet around an opening at the apex, widen somewhat in the basal region as they meet around the pentagonal base 70 μ in diameter having a raised border. Lime-shell glossy (illustrated specimen with debris adhering), gray or yellowish-gray.

Oospore black, glossy, ovoidal, with a peak at the apex, rounded at base, 500 μ long, 365 μ wide, 10 ridges in lateral view. Spirals narrow at the apical periphery widen and turn upward narrowing again to form a short peak at the apical center, meet with little change in width at basal pentagonal depression.

Previous Occurrence. (From Peck, 1957, p. 33) "Salt Wash member of the Morrison formation at Church Rock locality (USGS paleobotanical locality D289), San Juan County, Utah. Poorly preserved specimens that probably belong to this species were collected from the Morrison on the southern flank of the Maverick Springs anticline, Fremont County, Wyo."

Specimens Seen: *Illustrated:* oogonium (Plate 5, figs. 21-23), Slide 6-1, Franklin Co., Ind. *Not Illustrated:* oogonium and 2 oospores, Slide 6-1, Franklin Co., Ind.

5. Organ-genus OBTUSOCHARA Mädler, 1952

Obtusochara cylindrica Peck

Aclistochara cylindrica PECK, 1941, Jour. Pal., vol. 15, p. 291, pl. 42, figs. 38, 39, 41-44.

Obtusochara cylindrica PECK, 1957, U. S. Geol. Survey Prof. paper 294-A, p. 38, pl. 6, figs. 1-4.

Lime-shell without utricle and developed by 5 (4) spirals, obovoidal with flattened summit and protruding base, 8 intercellular ridges in lateral view, 700 μ long, 450-500 μ wide. Spirals narrow very little without a groove in the apical periphery, widen slightly as they turn onto the apical pole, meet at the apical center along a short line, approach the base with little change in width, slightly convex to slightly concave in the equatorial region, but more concave with intercellular ridges protruding at the basal depression which is 70 μ wide. Lime-shell well developed, glossy, off-white, surface punctate in one specimen (Plate 3, fig. 13). Another specimen (Plate 2, fig. 14) possessed an immature lime-shell, particulate in nature, which disintegrated when wet, allowing the organic remains of the 5 spiral cells to unwind as they were still pliable. The oospore described below was thus isolated.

Oospore dark brown, slightly obovoid, showing 8 ridges in lateral view, 570 μ long, 365 μ wide. Spirals decrease in width and are slightly concave forming a groove in the apical periphery, widen slightly as they approach the summit where they meet at a short line at the apical center, decrease slightly in width approaching the pentagonal base which is 70 μ in diameter. Surface glossy and punctate in reflected light.

In the legend for the original illustration of this species by Peck (op. cit.) as *Aclistochara cylindrica,* it is mentioned that the specimen, demonstrating seven intercellular ridges in lateral view, has only 4 spirals which is the same number demonstrated by one specimen in this report.

Previous Occurrence. (From Peck, 1957, p. 38) "Draney limestone and lower Bear River (Aptian) localities." The Bear River formation is in Wyoming, North America and the Draney limestone is in Idaho, North America, both from the Lower Cretaceous.

Specimens Seen: *Illustrated:* 5-spiralled oogonium (Plate 2, figs. 14-16) from which the oospore (Plate 2, figs. 17-19) was isolated, Slide 1-2, 4-spiralled oogonium (Plate 3, figs. 13-15), Slide 1-9, 1.1-2.1 ft. level of core, Erie Co., N. Y.

6. Organ-genus MAEDLERISPHAERA Horn af Rantzien, 1959 a

Maedlerisphaera ulmensis (Straub) Horn af Rantzien

Chara ulmensis STRAUB, 1952, Geol. Jahrb., vol. 66, p. 470, Taf. A, fig. 19.

Maedlerisphaera ulmensis (Straub) HORN AF RANTZIEN, 1959 a, Acta Univ. Stockholm., Stockholm Contrib. in Geol., vol. 4, no. 2, p. 100, pl. X, figs. 1-12.

Lime-shell without utricle and developed by 5 spirals, broadly ellipsoid (immature), with base and apex protruding, 560 μ long, 350 μ wide, 11 broad ridges in lateral view. Spirals slightly concave, narrowing slightly with some more concave and others less (forming depressions) at the apical periphery, widening to form a rosette with the spiral tips distinct, approaching the pentagonal base with little change in width, pentagonal base 50 μ wide. Lime-shell dull and particulate in nature.

This seems to fit the description of immature *Maedlerisphaera ulmensis,* except it is narrower which could indicate greater immaturity.

Previous Occurrence. (From Horn af Rantzien, 1959 a, p. 100) "Type locality. ———Between Ehingen and Ulm a. d. Donau, Wüttemberg-Hohenzollern, Germany. Type Stratum. ———Opfinger Schichten, Lower Freshwater Molasse, Oligocene. Stratigraphic Distribution. ———Oligocene (Middle Stampian upwards) sparsely up into the Miocene (Tortonian) (Mädler, 1955 b). Horizontal Distribution. ———Southern Germany, Switzerland."

Specimens Seen: *Illustrated:* oogonium (Plate 5, figs. 1-3) Slide 6-2, Steuben Co., Ind. *Not Illustrated:* 3 oogonia (top broken), Slide 6-2, Steuben Co., Ind.

7. Organ-genus GRAMBASTICHARA Horn af Rantzien, 1959 a

Grambastichara cylindrica (Mädler) Horn af Rantzien

Tectochara cylindrica MÄDLER, 1955, Geol. Jahrb., vol. 70, p. 295, Taf. 26, figs. 13-18.

Grambastichara cylindrica (Mädler) HORN AF RANTZIEN, 1959 a, Acta Univ. Stockholm., Stockholm Contrib. in Geol., vol. 4, no. 2, p. 74, pl. IV, figs. 7-11, pl. V, figs. 1-3.

Lime-shell without utricle and developed by 5 spirals, ellipsoid-elongate, with 12 distinct ridges in lateral view, summit rounded to truncate and protruding, basal pole protruding and truncate, 685-750 μ long, 400 μ wide. Spirals thick, slightly convex to slightly concave, very narrow and thin in the apical periphery where they are easily broken, without depressions in the apical periphery, widen considerably on the summit and thicken at the tips to form a rosette, meet at a very short line at the apex, widen considerably approaching the pentagonal base which is 50 μ in diameter. Lime-shell dull, punctate in reflected light, off-white or light brown.

Oospore black, dull, 500-585 μ long, 285-335 μ wide, 12 distinct ridges in lateral view, base narrowly truncate, summit broadly rounded to truncate. Spirals narrow and concave in the apical periphery, widen considerably on summit, meet at apex along a short line, widen considerably as they approach the small pentagonal base which is 50 μ wide. Surface punctate in reflected light.

Previous Occurrence. The material reported here seems to resemble an immature specimen with fluted protruding apical pole and a more mature specimen with rounded apical pole reported by Mädler (op. cit., Plate 26, fig. 17 and fig. 13 respectively—the immature specimen is slightly more developed than in fig. 17, but not quite as mature as in fig. 16) as *Tectochara cylindrica* from the Oligocene. In Southern Germany, this species was found in the Aquatanian, while in Switzerland, it came from the middle Stampian, Mädler mentions the similarity to this species of *Chara subcylindrica* from the upper Eocene, Lower Headon Beds, England. Horn af Rantzien (op. cit.) transferred *Chara subcylindrica* to *Granbastichara subcylindrica* as a new combination, but was uncertain that this species should be separate from *G. cylindrica.*

Specimens Seen: *Illustrated:* oospore (Plate 1, figs. 1-3), Slide 3-6, 2.1-2.9 ft. level of core, Erie Co. N. Y.; oogonium (Plate 3, figs. 4-6) sacrificed, oogonium (Plate 3, figs. 7-9) Slide 1A-5, 1.1-2.1 ft. level of core, Erie Co., N. Y. *Not Illustrated:* oogonium, Slide 1-3, 3 oogonia and an oospore (isolate), Slide 1-7, 1.1-2.1 ft. level of core, Erie Co. N. Y.

Genus TOLYPELLA von Leonhardi, 1863

Tolypella sp.

Oospore terete (with one side damaged), spheroidal with broadly rounded poles, 385 μ long, 365 μ wide (because of damage, this is slightly greater than actual size), 10 prominent ridges. Spirals narrow, narrowing only slightly at apical periphery, widening slightly before narrowing to meet at a point at the apical center, width varies little along the whole length of the spirals except where they taper at the apical ends, appear grooved at the apex because the prominent ridges cast shadows, meet at the pentagonal base 80 μ in diameter. The outer colored membrane dark brown, opaque and minutely punctate in reflected light. The nature of the outer colored membrane in transmitted light, outer spiral elements (with or without calcification), coronula, and exact size and shape (damaged) are unknown. Therefore, it seems desirable to refer this specimen without species designation to the genus *Tolypella,* although it is probably *Tolypella prolifera.*

Previous Occurrence. (From Horn af Rantzien, 1959 b, p. 213) "The first gyrogonites referred to *Tolypella* were from the Lower Headon Beds of England (Reid and Groves, 1921). These beds are referred to the Upper Bartonian (uppermost Eocene). Groves (1926, p. 173) referred a species from the Lattorfian (Oligocene) Bembridge Beds of England (see Gignoux, op. cit.) to this genus. Mädler (1952, pp. 30-36) referred four Kimmeridgian (Upper Jurassic) gyrogonite species from Germany to *Tolypella;* he also noticed that certain gyrogonites described from the Bartonian (Eocene) of the Paris Basin and from the Morrison Formation (Upper Jurassic) of the Rocky Mountains should preferably be included. The same author (1955, pp. 307-308) described and discussed two gyrogonite species of *Tolypella,* from the Chattian (Oligocene) and Tortonian (Miocene) of southern Germany and Switzerland."

This is a recent genus and the species *Tolypella prolifera,* to which it seems the oospore reported here is most closely allied, has been reported for Canada and New York among many records. It comes from Lake Huron and Lake Ontario as well as other lakes and ponds primarily, as well as from a river pond and roadside ditch.

Specimen Seen: *Illustrated:* oospore (Plate 1, figs. 25-27), Slide 3-5, 2.1-2.9 ft. level of core, Erie Co., N. Y.

VEGETATIVE REMAINS

Organ-genus CHARAXIS Harris, 1939

Charaxis sp.

All vegetative material found was so fragmentary that reconstruction of the plant would be very difficult. There were broken nodal and internodal sections of stems and branchlets with the critical characteristics discernible similar to modern charophytes. All such material is referred to *Charaxis* sp. Harris (1939, p. 67).

Plate 1, fig. 10, see following paragraph.

Plate 1, fig. 14, shows a surface view of a stem internode with the bases of broken spine cells in a cluster appearing as dots in the lower left part of the figure particularly and scattered elsewhere. A cross sectional view of the same stem shown in Plate 1, fig. 10 is 535 μ in diameter. The lumen of the larger cortex cells is 65 μ in diameter, of smaller cells 50 μ. A cross section across the bases of three spine cells in a cluster is seen at the upper edge of the stem section. There are 11 cortical cells surrounding the central cylinder. *Illustrated Specimen:* stem fragment, Box 1, 2.1-2.9 ft. level of Core 3, Erie Co., N. Y.

Plate 1, fig. 18, shows a broken corticated branchlet internode 250 μ in diameter. The internodal meeting of the cortex cells is seen near the mid-point of the internode. From the number of cells contained in the section, it would appear that this is a diplostichously corticated branchlet fragment. *Illustrated Specimen:* branchlet internodal fragment, Box 1, 1.1-2.1 ft. level of Core 3, Erie Co., N. Y.

Plate 2, fig. 1, illustrates a stem fragment with a broken nodal portion at mid-section, but little can be told about the node since the exterior is so heavily encrusted. The stem is 420 μ in diameter with erratically occurring frequent openings in the cortex. The openings are variable in diameter and are probably not all former spine cell locations, but some of them are probably the result of damage by natural causes. *Illustrated Specimen:* stem fragment, Box 1, 1.1-2.1 ft. level of Core 3, Erie Co., N. Y.

Plate 2, fig. 2, is of a stem cross section 335 μ in diameter, 200 μ across the central cell lumen and about 17 μ across the lumen of the smaller cortex cells. Altogether there are 16 cortex cells. Spine cell pattern is not discernible. *Illustrated Specimen:* stem fragment, Box 1, 1.1-2.1 ft. level of Core 3, Erie Co., N. Y.

Plate 2, fig. 3, is an interior view of a fragment of branchlet cortex from an internodal area showing the meeting of the cortical cells in a similar way to modern charophytes. Plate 2, fig. 5, is a less enlarged view of the exterior surface of the same branchlet fragment showing diplostichous cortication common among modern charophytes. *Illustrated Specimen:* Branchlet fragment, Box 1, 1.1-2.1 ft. level of Core 3, Erie Co., N. Y.

Plate 2, fig. 4, is another stem cross section similar to that shown in Plate 1, fig. 10, but less enlarged. *Illustrated Specimen:* stem section, Box 1, 1.1-2.1 ft. level of core 3, Erie Co., N. Y.

Plate 2, fig. 5, please see Plate 2, fig. 3 above.

Plate 2, fig. 10, illustrates the cross section of a stem bearing single, long spine cells. The base of one can be seen well at the lower side of the specimen. Eighteen cortical cells differing slightly in size surround the central cylinder, the lumen of which is 285 μ in diameter. This probably is similar to some long-spined forms of *Chara contraria* which is diplostichously corticated with the primary cells prominent, but not much larger than the secondary cells. Cells of the secondary series sometimes slip past one another adding a cell or two to the normal number of 16 cortical cells altogether surrounding the central cylinder. The fossil stem is about 500 μ in diameter which compares favorably with *Chara contraria,* too. *Illustrated Specimen:* stem fragment, Box 1, 1.1-2.1 ft. level of core 3, Erie Co., N. Y.

Plate 4, figs. 12 and 13, illustrate material very similar to the stem fragment illustrated in Plate 1, fig. 14 and Plate 1, fig. 10. This cross section shows 12 cortex cells, however, and the section is 500 μ in diameter. *Illustrated Specimen:* stem fragment, Slide 2-1, 0-1.1 ft. level of core 3, Erie Co., N. Y.

Plate 4, fig. 11, is a cross sectional view of a stem fragment. It is 435 μ across section, 250 μ across the lumen of the central cell and 65 μ across the largest cortical cells, 50 μ across the smallest cortical cells. There are 16 cortical cells around the central cell with the primary prominent and bearing long spine cells. This is similar to a long-spined *Chara contraria. Illustrated Specimen:* stem fragment, Slide 2-6, 0-1.1 ft. level of core 3, Erie Co., N. Y.

Plate 4, fig. 20 and Plate 5, fig. 11, are a surface and cross sectional view, respectively, of a stem fragment similar to that shown in Plate 2, fig. 10, having 18 cortical cells and long single spine cells. This stem is 420 μ in diameter with the cortex cells varying from the median of 50 μ for the size of the lumina. *Illustrated Specimen:* stem fragment, Slide 2-1, 0-1.1 ft. level of core 3, Erie Co., N. Y.

Previous Occurrence. This artificial genus was established for fossil vegetative materials agreeing in so far as known with the living Genus *Chara.* Due to the fragmentary nature of the material, it would be hazardous to refer any of it to a species of *Chara.* However, there appear to be stems with diplostichous, irregularly haplostichous, and possibly irregularly triplostichous arrangements of the cortex, and some diplostichous branchlets. Spines range from single to fascicles of several, and apparently long to short. The first material assigned to this genus was from the British Purbeck, upper Jurassic.

SUMMARY AND CONCLUSIONS

Glacial and post-glacial deposits in New York and Indiana are described and charophytes as well as some associated fossils which were isolated from samplings are listed. Fossil charophytes were represented by lime-shells, oospores and fragmentary vegetative material. Methods of isolating and photographing them are given. The structure of an extant species of charophyte, *Chara contraria,* is given with a discussion of terminology. A key to the lime-shell characteristics representing seven genera, twelve species and one variety of fossil charophytes found is included with descriptions and illustrations of the species and variety. An oospore lacking a lime-shell and some vegetative remains represent two more genera described and illustrated. A new species of *Clavatorites* and *Latochara* are included and a new combination is formed.

The variety of charophytes reported here should stimulate interest in a neglected field. Chronologically, several genera are extended into glacial and post-glacial time which were known only from older deposits.

Since oospores were preserved in these collections, their study adds to the knowledge of some of the species described from older deposits in which oosporal remains were missing, fragmentary or were known only from sectional study of oogonia and membrane fragments. Further study of glacial and post-glacial deposits in which oospores may be preserved offers possibilities to enlarge the knowledge of older genera.

Fossil representatives of extant species associated with strictly fossil species of charophytes as reported here gives an interesting ecological tool to apply to the latter.

Variation in the occurrence of decoration from individual to individual and in different areas of the same oogonium emphasizes the limitation in the use of this characteristic in systematics.

Variation in the number of spiral cells in lime-shells of a species emphasizes the limitation of use of this characteristic in systematics, also. Four and six-spiralled lime-shells were found in species normally having five spiral cells.

BIBLIOGRAPHY

Allen, G. O. 1951. Notes on charophytes from British Columbia. Proc. Linnean Soc. London, session 162, pt. 2, 1949-50, pp. 148-152.

Allen, T. F. 1882. Development of the cortex in Chara. Torrey Bot. Club, Bull., vol. 9, no. 4, pp. 37-47, pls. 15-22.

Braun, A. 1845. In Engelmann and Gray—Plantae Lindheimerianae. Boston Jour. Nat. Hist., vol. 5, p. 264.

Daily, F. K. 1944. The Characeae of Nebraska. Butler Univ. Bot. Stud., vol. 6, pp. 149-171.

———. 1953. The Characeae of Indiana. Ibid., vol. 11, pp. 5-47.

Gignoux, M. 1950. Geologie Stratigraphique. Paris: ed. 4, pp. 1-735, 155 figs.

Groves, J. and Bullock-Webster, G. R. 1920. The British Charophyta. London: Ray Soc., vol. 1, pp. vii-141, 25 figs., 20 pls.

Groves, J. 1926. In E. M. Reid and M. E. J. Chandler—Charophyta. Cat. of Cainozoic Plants in British Mus. of Nat. Hist., vol. 1, pp. 165-197, 5 figs., 1 pl.

Harris, T. M. 1939. British Purbeck Charophyta. London: British Mus. of Nat. Hist. pp. v-83, figs. 1-16, pls. 1-17.

Horn af Rantzien, H. 1950. Charophyta reported from Latin America. Kungl. Svenska Vet. Ak., Arkiv f. Bot. ser. 2, bd. 1, no. 8, pp. 355-411.

———. 1951. On the fossil Charophyta of Latin America. Svensk Bot. Tidskr., vol. 43, no. 4, pp. 658-677, Uppsala.

———. 1954. Middle Triassic Charophyta of South Sweden. Opera Bot. (suppl. ser. of Bot. Notiser), vol. 1, no. 2, pp. 1-83, 7 pls.

———. 1956. Morphological terminology relating to female gametangia and fructifications. Bot. Notiser, vol. 109, no. 2, pp. 212-259.

———. 1959a. Morphological types and organ-genera of Tertiary charophyte fructifications. Acta Univ. Stockholm., Stockholm Contrib. in Geol., vol. 4, no. 2, pp. 45-197, 21 pls.

———. 1959b. Recent charophyte fructifications and their relations to fossil charophyte gyrogonites. Kungl. Svenska Vet. Ak., Arkiv f. Bot., ser. 2, bd. 4, no. 7, pp. 165-332, 19 pls.

Kützing, F. T. 1845. Phycologia Germanica. Nordhausen: pp. 255-260.

Leonhardi, H. von. 1863. Die Böhmischen Characeen. Lotos, vol. 13, pp. 55-80, 110-111.

Linnaeus, C. 1753. Species Plantarum. Stockholm: vol. 2, pp. 1156-7.

Mädler, K. 1952. Charophyten aus dem nordwestdeutschen Kimmeridge. Geol. Jahrb., bd. 67, pp. 1-46, 2 figs., 8 pls.

———. 1955. Zur Taxionomie der Tertiären Charophyten. Geol. Jahrb., vol. 70, pp. 265-328, pls. 23-26.

Peck, R. E. 1937. Morrison Charophyta from Wyoming. Jour. Pal., vol. 11, pp. 83-90, pl. 14.

———. 1941. Lower Cretaceous Rocky Mountain non-marine microfossils. Jour. Pal., vol. 15, pp. 285-304. 3 pls.

———. 1957. North American Mesozoic Charophyta. Geol. Survey Prof. Paper 294-A, U. S. Printing Office, Washington, D. C., pp. 1-44, 8 pls., 7 text-figures.

Prescott, G. W. 1951. Algae of the Western Great Lakes area. Cranbrook Inst. of Sci. Bull., vol. 30, pp. 1-946.

Reid, C. and Groves, J. 1921. The Charophyta of the Lower Headon Beds of Hordle (Hordwell) Cliffs (South Hampshire). Quart. Jour. Geol. Soc. London, vol. 77, pt. 3, no. 307, pp. 175-192, 3 pls.

Robinson, C. B. 1906. The Chareae of North America. Bull. New York Bot. Gard., vol. 4, no. 13, pp. 244-308.

Ross, C. A. 1960. Population study of charophyte species, Morrison formation, Colorado. Jour. Pal., vol. 34, no. 4, pp. 717-726.

Rubin, M. and Alexander, C. 1960. U. S. Geological Survey radiocarbon dates V. Amer. Jour. Sci., Radiocarbon Suppl., vol. 2, pp. 129-185.

Straub, E. W. 1952. Mikropalaöntologische Untersuchungen im Tertiär zwischen Ehingen und Ulm a. d. Donau. Geol. Jahrb., vol. 66, pp. 433-523, Taf. 4, Texttaf. A-C, Abb. 1-24, Hannover.

Suess, H. E. 1954. U. S. Geological Survey radiocarbon dates I. Science, vol. 120, pp. 467-473.

Wayne, W. J. and Thornbury, W. D. 1955. Wisconsin stratigraphy of northern and eastern Indiana. Guidebook, 5th Bienn. Pleistocene Field Conf., State Geol. Survey of Indiana and Ohio, pp. 1-34.

Wood, R. D. 1949. The Characeae of Woods Hole region, Massachusetts. Biol. Bull., vol. 96, no. 2, pp. 179-203.

Wood, R. D. and Muenscher, W. C. 1956. The Characeae of the State of New York. Agr. Exp. Sta. of the New York Col. of Agr., Cornell Univ., Mem., no. 338, pp. 1-77, 18 pls.

EXPLANATION OF PLATES

PLATE 1

Fossil charophytes from the 2.1-2.9 ft. level of core 3, Erie Co., N. Y., except Fig. 18 which is from the 1.1-2.1 ft. level of core.

FIGURES 1-3. *Grambastichara cylindrica* (Mädler) Horn af Rantzien
Oospore: 1, lateral view; 2, basal view; 3, apical view. 40X.

FIGURES 4-6. *Charites strobilocarpa* (Reid and Groves) Horn af Rantzien
Oospore isolated from oogonium in figs. 7-9: 4, lateral view; 5, apical view; 6, basal view. 43 X.

FIGURES 7-9. *Charites strobilocarpa* (Reid and Groves) Horn af Rantzien
Oogonium: 7, lateral view; 8, apical view; 9, basal view; 7 inset, another view of basal plug of oospore seen in fig. 4. 43 X.

FIGURE 10. *Charaxis* Harris
Cross section of stem fragment seen also in Plate 1, fig. 14. 43 X.

FIGURES 11-13. *Chara contraria* A. Braun ex Kützing
Broken oogonium: 11, lateral view; 12, apical view; 13, basal view. 43 X.

FIGURE 14. *Charaxis* Harris
Surface view of a stem fragment. 26X.

FIGURES 15-17. *Charites strobilocarpa* var. *ellipsoidea* (Reid and Groves) Daily, nov. comb.
Four-spiralled oospore: 15, lateral view; 16, apical view; 17, basal view. 43X.

FIGURE 18. *Charaxis* Harris
Branchlet internodal fragment. 71X.

FIGURES 19-21. *Chara contraria* Braun ex Kützing
Oospore isolated from oogonium shown in Plate 1, figs. 11-13: 19, lateral view; 20, basal view with plug; 21, basal view without plug. 43X.

FIGURES 22-24. *Chara evoluta* T. F. Allen
Oospore: 22, lateral view; 23, apical view; 24, basal view. 43X.

FIGURES 25-27. *Tolypella* sp.
Oospore: 25, lateral view; 26, apical view; 27, basal view. 43X.

FIGURES 28-30. *Chara evoluta* T. F. Allen
Oospore: 28, lateral view; 29, basal view; 30, apical view. 43X.

PLATE 2

Figs. 6-8. Fossil charophytes from the 2.1-2.9 ft. level of core 3, Erie Co., N. Y.

Figs. 1-5 and 9-28. Fossil charophytes from the 1.1-2.1 ft. level of core 3, Erie Co., N.Y.

FIGURE 1. *Charaxis* Harris
Stem fragment. 26X.

FIGURE 2. *Charaxis* Harris
Stem cross section. 43X.

FIGURE 3. *Charaxis* Harris
Fragment of cortex from a branchlet internode. 32X.

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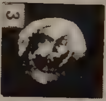
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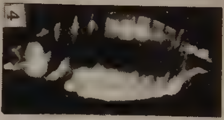
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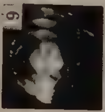
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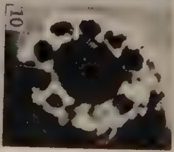
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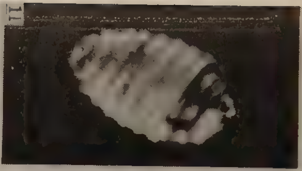
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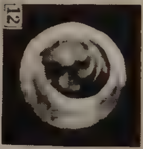
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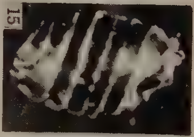
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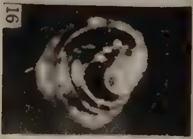
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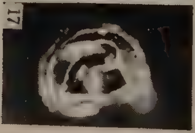
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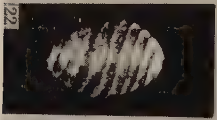
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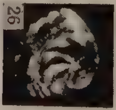
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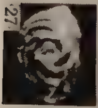
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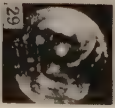
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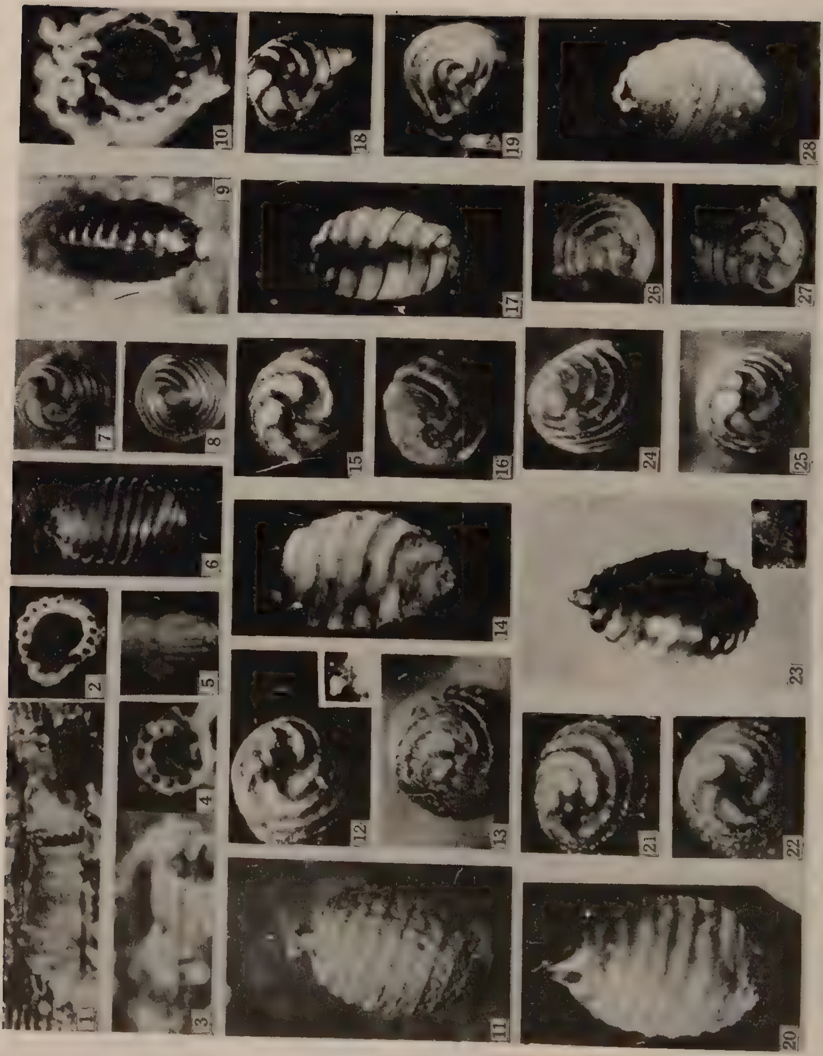
FIGURE 4. *Charaxis* Harris
Stem cross section. 26X.
FIGURE 5. *Charaxis* Harris
Branchlet cortex fragment showing a nodal area. 15X.
FIGURES 6-8. *Chara contraria* Braun ex Kützing
Oospore: 6, lateral view; 7, apical view; 8, basal view. 43X.
FIGURE 9. *Charites bitruncata* (Reid and Groves) Horn af Rantzien
Oospore in lateral view. 43X.
FIGURE 10. *Charaxis* Harris
Stem cross section. 43X.
FIGURES 11-13. *Latochara Waynei* Daily, new species
Oogonium, holotype: 11, lateral view; 12, apical view; 13, basal view. 43X.
FIGURES 14-16. *Obtusochara cylindrica* (Peck) Peck
Oogonium: 14, lateral view; 15, apical view; 16, basal view. 43X.
FIGURES 17-19. *Obtusochara cylindrica* (Peck) Peck
Oospore isolated from the oogonium shown plate 2, figs. 14-16; 17, lateral view; 18, apical view; 19, basal view. 43X.
FIGURES 20-22. *Latochara Waynei* Daily, new species
Oogonium, co-type: 20, lateral view; 21, basal view; 22, apical view. 43X.
FIGURES 23-25. *Latochara Waynei* Daily, new species
Oospore isolated from the oogonium shown in plate 2, figs. 20-22: 23, lateral view; 24, basal view; 25, apical view. 43X. 23, inset, is a piece of the outer colored membrane of the oospore. 307X.
FIGURES 26-28. *Chara evoluta* T. F. Allen
Oospore: 26, basal view; 27, apical view; 28, lateral view. 43X.

PLATE 3

Fossil charophytes from the 1.1-2.1 ft. level of core 3, Erie Co., N. Y.
FIGURES 1-3. *Charites strobilocarpa* var. *ellipsoidea* (Reid and Groves) Daily, new combination
Four-spiralled oogonium: 1, lateral view; 2, basal view; 3, apical view. 43X.
FIGURES 4-6. *Grambastichara cylindrica* (Mädler) Horn af Rantzien
Oogonium: 4, lateral view; 5, apical view; 6, basal view. 43X.
FIGURES 7-9. *Grambastichara cylindrica* (Mädler) Horn af Rantzien
Oogonium: 7, lateral view; 8, apical view; 9, basal view. 43X.
FIGURES 10-12. *Charites strobilocarpa* var. *ellipsoidea* (Reid and Groves) Daily, new combination
Five-spiralled oogonium: 10, lateral view; 11, apical view; 12, basal view. 43X.
FIGURES 13-15. *Obtusochara cylindrica* (Peck) Peck
Broken oogonium: 13, lateral view; 14, apical view; 15, basal view. 43X.
FIGURES 16-18. *Charites strobilocarpa* var. *ellipsoidea* (Reid and Groves) Daily, new combination
Six-spiralled oogonium: 16, lateral view; 17, basal view; 18, apical view. 43X.
FIGURES 19-21. *Chara sejuncta* Braun
Oogonium: 19, lateral view; 20, apical view; 21, basal view. 43X.

PLATE 4

Figs. 1-3. Fossil charophytes from the 1.1-2.1 ft. level of core 3, Erie Co., N. Y.
Figs. 4-20. Fossil charophytes from the 0-1.1 ft. level of core 3, Erie Co., N. Y.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FIGURES 1-3. *Chara sejuncta* Braun
Oospore isolated from oogonium shown in plate 3, figs. 19-21: 1, lateral view; 2, apical view; 3, basal view. 43X.

FIGURE 4. *Charites bitruncata* (Reid and Groves) Horn af Rantzien
Oogonium in lateral view. 43X.

FIGURES 5-7. *Charites bitruncata* (Reid and Groves) Horn af Rantzien
Oospore isolated from oogonium in plate 4, fig. 4: 5, lateral view; 6, apical view; 7, basal view. 43X.

FIGURES 8-10. *Latochara Waynei* Daily, new species
Oogonium, co-type: 8, lateral view (32X); 9, basal view (15X); 10, apical view (15X).

FIGURE 11. *Charaxis* Harris
Stem cross section. 26X.

FIGURES 12 and 13. *Charaxis* Harris
Stem fragment: 12, cross section (43X); 13, surface view (32X).

FIGURES 14-16. *Charites bitruncata* (Reid and Groves) Horn af Rantzien
Oogonium: 14, lateral view; 15, apical view; 16, basal view. 43X.

FIGURES 17-19. *Charites strobilocarpa* var. *ellipsoidea* (Reid and Groves) Daily, new combination
Oogonium: 17, lateral view; 18, apical view; 19, basal view. 43X.

FIGURE 20. *Charaxis* Harris
Stem fragment, surface view. 43X. (Cross section of the same fragment of stem shown plate 5, fig. 11.)

PLATE 5

Fossil charophytes: Figs. 1-6 and 10 from Steuben Co., Ind.: Figs. 7-9, from the 15-15½ ft. level of core, edge of Cass Lake, LaGrange Co., Ind.; Fig. 11, 0-1.1 ft. level of core 3, Erie Co., N. Y.; Figs. 12-17, from Noble Co., Ind.; Figs. 18-26, from Franklin Co., Ind.

FIGURES 1-3. *Maedlerisphaera ulmensis* (Straub) Horn af Rantzien
Oogonium: 1, lateral view; 2, apical view; 3, basal view. 43X.

FIGURES 4-6 and 10. *Chara evoluta* T. F. Allen
Oospore: 4, lateral view; 5, apical view; 6, basal view. 43X. 10, Outer colored membrane. 307X.

FIGURES 7-9. *Charites bitruncata* (Reid and Groves) Horn af Rantzien
Oospore: 7, basal view; 8, lateral view; 9, apical view. 43X.

FIGURE 11. *Charaxis* Harris
Stem fragment, cross section. 43X. (Same fragment of stem as shown in surface view plate 4, fig. 20.

FIGURE 12, left. *Charites strobilocarpa* var. *ellipsoidea* (Reid and Groves) Daily, new combination
Oospore in lateral view. 43X.

FIGURE 12, right. *Clavatorites noblensis* Daily, new species
Oospore in lateral view. 43X.

FIGURE 13. *Charites strobilocarpa* (Reid and Groves) Horn af Rantzien
Oospore, lateral view. 43X.

FIGURE 14. *Clavatorites noblensis* Daily, new species
Oospore, lateral view. 43X.

FIGURES 15-17. *Clavatorites noblensis* Daily, new species
Oogonium, holotype: 15, lateral view; 16, apical view; 17, basal view. 43X.

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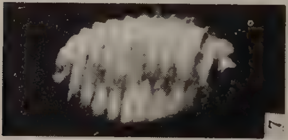
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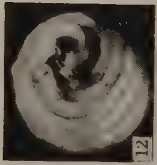
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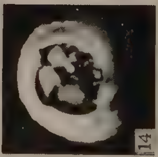
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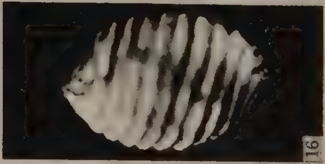
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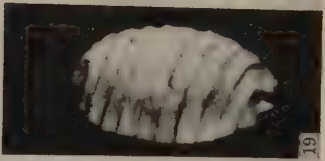
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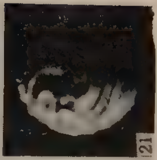
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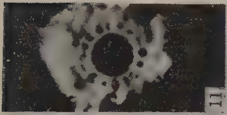
FIGURES 18-20. *Chara sejuncta* Braun
Oogonium: 18, lateral view; 19, apical view; 20, basal view. 43X.
FIGURES 21-23. *Latochara spherica* Peck
Oogonium: 21, lateral view; 22, apical view; 23, basal view. 43X.
FIGURES 24-26. *Latochara latitruncata* (Peck) Mädler
Oogonium: 24, lateral view; 25, apical view; 26, basal view. 43X.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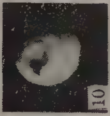
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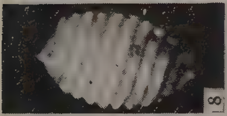
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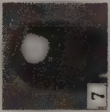
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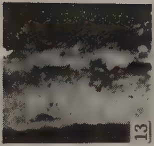
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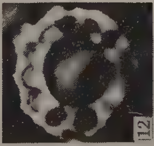
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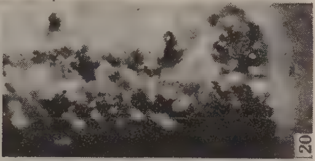
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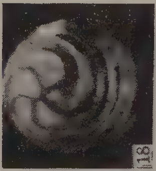
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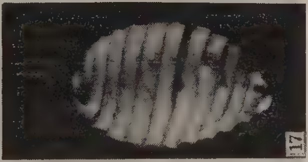
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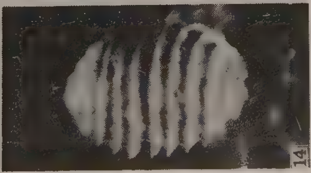
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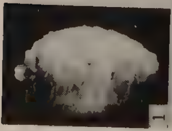
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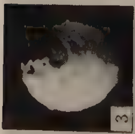
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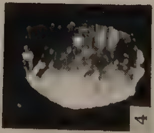
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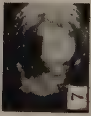
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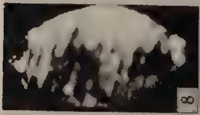
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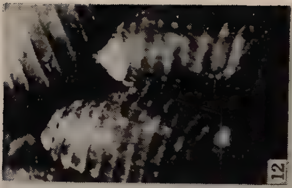
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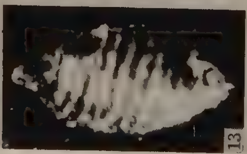
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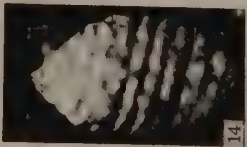
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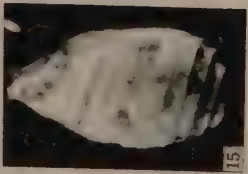
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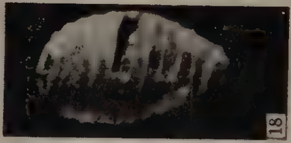
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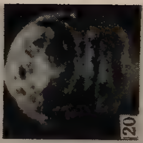
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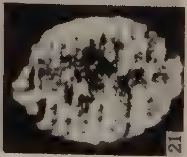
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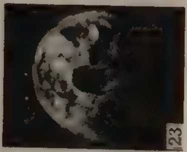
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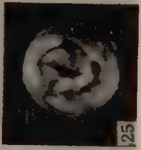
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NOTES ON CULTIVATED JUNIPERS

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INTRODUCTION

The genus *Juniperus* is the third largest in the coniferales, and its many species are not only widespread but also extensively cultivated. Several factors make the classifying of horticultural junipers both difficult and confusing. First, the species are ill-defined since there are few good key characters and few qualitative characters. The numerous quantitative characters vary considerably. The characteristics of the reproductive organs, fruit characters, vary as much as those of the vegetative body. Secondly, natural hybridization at the species level is widespread and the recombinations are occasionally bizarre. Thirdly, horticultural selection is made by man without concomitant analysis of the variability of the populations at the site. Thus, it is often difficult to determine just which species a variety should be referred to. Fourthly, many of the selections are based on odd growth habit or aspect, low growing, cup-shaped, vase-shaped, upright, etc., and growth form is controlled in some cases by single gene differences, in others by polygenes. If the growth form is selected from a fairly pure population it is easy to label, if it comes from a hybrid swarm such a plant may be virtually impossible to properly associate with its progenitors once it is removed from the site. Because of these problems, selections of junipers to receive horticultural names should be accompanied by careful analyses of their origins. This is not so difficult as it sounds, at least not for a specialist in the group. The name *Juniperus* properly applies to those members of the family Cupressaceae with small, usually dark, fleshy, berry-like pistillate cones containing seeds without wings. The staminate and pistillate cones may be borne on the same plant (monoecious) or, more characteristically, on different plants (dioecious), even though the strongly dioecious species occasionally produce monoecious individuals, apparently at random. The junipers may very well be the most plastic of the cone bearing plants. They may be "forced" or trained to take innumerable shapes, many quite grotesque.

I would estimate that the genus probably contains about forty species even though over sixty have been described. Geologically, the more primitive junipers are known from the Upper Cretaceous of New England and Green-land, while the more recent arid lands' junipers are known from the Pliocene and the Pleistocene. The arid lands' types have probably evolved with the development of our modern deserts, apparently during the late Cenozoic. The majority of the species, the appressed scale-leaved ones, are characteristically found in semi-arid regions or in arid regions of mid-altitudes. The most primitive species, *J. drupacea* Labill., *J. Oxycedrus* L., and perhaps *J. foetidissima* Willd., are found in the arid areas of Asia Minor and from Morocco through Spain to the Caucasus. Other species are found from the Pamirs to Japan and Korea. In North America, junipers are found widely from Canada and Alaska south through Mexico into Central America. The most widespread species is the circumboreal *J. communis* L.. The only species extending into the southern hemisphere is the African *J. procera* Hockst., which is an important forest tree at median to high altitudes from Ethiopia to northern Tanganyika. In the United States the most widespread species is *J. virginiana* L., especially so, if *J. scopulorum* Sarg. and *J. silicicola* (Small) L. H. Bailey (*barbadensis* of American authors) are considered as subspecies of it, a concept which I do not feel is justified by the data, however.

On each continent most of the species are centered about the Pacific side and are nearly equally divided between Eurasia and America. The present distribution of *Juniperus* fits Buchholz' idea that the Pacific perimeter probably represents the distribution center of the Coniferales during most of their recent period of evolution.

The conservative treatment of the genus calls for three sections: Caryocedrus, Oxycedrus, and Sabina. The sections show structural series with regard to female cones and leaf types. The transitions are from more woody cones in section Caryocedrus to quite fleshy berry-cones in section Oxycedrus, and from the acicular-type (awl shaped) leaves to reduced scale-type leaves in section Sabina.

SYNOPSES OF THE SECTIONS IN *JUNIPERUS*

CARYOCEDRUS. Microsporangiate strobili clustered 3 to 6 in a head, spreading after anthesis, their axes stipitate; microsporophylls 9 to 12, their connectives ovate acute, incurved at the apex; seeds joined into a thick globose woody 3-angled mass; leaves acicular.

The single species, *J. drupacea* Labill., may represent a relatively unsuccessful attempt at evolution toward a woody-coned arid lands' plant, or it may represent the sole surviving species of a more ancient type of juniper. This species is found in the eastern Mediterranean from the arid mountainsides of southern Turkey, to Syria, Lebanon, and the Peloponnesos.

The evidence from wood anatomy and from gross morphology suggest that Labillardière (1791) was correct in placing this species in the genus *Juniperus*. Antoine's and Kotschy's evidence (1854) for the genus *Arceuthos* does not satisfy me. Kaiser (1954) stated, "From the microstructural study of the mature wood it is concluded that this species is more similar to *Juniperus* than to any other genus of the Cupressaceae. This conclusion is based upon the combination of the following characteristics: 1) Ray parenchyma with a) horizontal walls relatively thick; b) abundant primary pit-fields in horizontal walls; c) indentures regularly present; d) end-walls nodular; and 2) Wood parenchyma with nodular transverse walls." The overall differences between *J. drupacea* in section Caryocedrus from those of *J. Oxycedrus* of section Oxycedrus are only slightly greater than those of *J. Oxycedrus* from *J. sabina* of section Sabina. As for the woody cones of *J. drupacea,* some very nearly woody cones occur in some of our xerophytic junipers of southwestern United States and Mexico.

OXYCEDRUS. Strobili axillary; microsporangiate strobili solitary with stipitate axes, the stipes covered with minute scale-like bracts; microsporophylls decussate; ovules three, alternate with the inner scales of the strobilus, their enlarged stigma-shaped tips persistent on the fruits; seeds free, usually three, fewer by abortion; leaves ternate, linear, acicular, free and jointed at the base, eglandular, channeled and white-glaucous on the upper surface; buds scaly.

There are nine species commonly listed for section Oxycedrus or probably seven by a more conservative treatment. A conservative list includes *J. Oxycedrus* L. (containing *J. macrocarpa* Sibth. & Sm. and *J. Cedrus* Webb & Berth.), *J. brevifolia* Antoine, *J. taxifolia* Hook. & Arn., *J. formosana* Hayata, *J. rigida* Sieb. & Zucc., *J. conferta* Parl., and *J. communis* L..

J. Oxycedrus, J. macrocarpa, J. Cedrus and *J. brevifolia* are very closely related with the latter species apparently the most divergent.

J. formosana and *J. taxifolia* are likewise closely related.

J. communis, J. rigida, and *J. conferta* form a final close species group in the section.

SABINA. Strobili terminal on dwarf axillary branches; microsporangiate strobili solitary; microsporophylls ternate or opposite; seeds 1-12, free; leaves ternate or opposite, mostly scale-like, closely appressed, crowded and adnate on the branches, glandular or eglandular; leaves on vigorous branches or young plants free and acicular.

The Sabina section, the largest of the three, contains about thirty species judged by quite conservative estimates even though more than fifty are listed in current taxonomy. These species are about equally divided between the New and the Old World. Most of the New World species are found in the more mesic habitats within and at the edges of the North American deserts. In the Old World most of the species occur in arid areas from the Mediterranean across Asia Minor to Kashmir and the Himalayas. A conservative list of the species in the Sabina section would be as follows: New World—*J. bermudiana* L., *J. virginiana* L. (including *J. scopulorum* Sarg., *J. silicicola* (Small) L. H. Bailey, as subspecies), *J. lucayana* Britton (including *J. gracilior* Pilger, *J. saxicola* Britt. & Wilson), *J. horizontalis* Moench, *J. Ashei* Buchholz, *J. californica* Carr. (including *J. utahensis* (Engelm.) Lemmon), *J. monosperma* (Engelm.) Sarg. (including *J. Pinchoti* Sudw., *J. erythrocarpa* Cory), *J. comitana* Martinez, *J. Gamboana* Martinez, *J. Deppeana* Steud., *J. Patoniana* Martinez, *J. flaccida* Schl., *J. jaliscana* Martinez, *J. Blancoi* Martinez, *J. monticola* Martinez, *J. Standleyi* Steyermark, *J. durangensis* Martinez; Old World—*J. procera* Hockst., *J. squamata* Lamb. (including *J. recurva* Buch.-Ham.), some fifteen Asiatic one-seeded junipers which probably represent about four species not clearly known, *J. phoenicea* L., *J. foetidissima* Willd., *J. chinensis* L., *J. semiglobosa* Regel, *J. davurica* Pall., *J. excelsa* Bieb., and *J. thurifera* L.

In the New World species there are some close affinities suggesting considerable introgression and possibly occasional swamping of genetic differences whenever they do develop. *J. virginiana* apparently hybridizes freely with *J. scopulorum, J. lucayana,* and *J. Ashei. J. silicicola* is apparently a population of introgressants between *J. virginiana* and *J. lucayana. J. Ashei* and *J. lucayana* are considerably more distinct from *J. virginiana* than is *J. scopulorum.*

J. horizontalis, widespread across the north in the New World, is very closely related to *J. Sabina, J. semiglobosa,* and *J. davurica* of the Old World. This group needs population analyses.

J. monosperma forms intermediates with *J. comitana, J. Ashei,* and *J. californica (utahensis),* and with *J. Deppeana.* Some of the supposed introgressants have been given specific names. For example, what once was *J. monosperma* has differentiated into a very variable species complex caused primarily by hybridization and introgression with other species, particularly *J. Deppeana, J. californica (utahensis),* and *J. scopulorum. J. Pinchoti* Sudw. is a race of introgressants between *J. Deppeana* and *J. monosperma. J. texensis* van Melle is a backcross race of upright introgressants in this complex to *J. Deppeana. J. erythrocarpa* Cory is a segregated form from this complex between *J. Pinchoti* and *J. Deppeana.* Analyses of population variation make these points quite clear. The author has engaged in quite detailed studies of variation in this complex to be published elsewhere.

The relationships between *J. monticola, J. Standleyi,* and *J. durangensis* need clarification.

The relationship between *J. scopulorum* and *J. jaliscana* with distinct ranges but very similar morphology needs study.

Very little is known about the Old World junipers with respect to population dynamics. There are some highly variable species such as *J. chinensis,* *J. excelsa, J. squamata,* but the entire area needs thorough study. It is to be expected that considerable hybridization has occurred and that numerous hybrid swarms exist from which many clones may have been selected.

With an eye for the complexities of juniper evolution, we should take a look at our cultivated ones. Since we do not know where all of them fit in, we should probably accept a very conservative treatment until the facts are available. On that basis, I present the following notes and keys to the cultivated junipers.

COMPLICATIONS IN CLASSIFYING CULTIVATED JUNIPERS

It is not easy to learn the junipers used in horticulture. The first complicating factor is a biological one, namely, that the species, as they are now known within both sections Oxycedrus and Sabina, hybridize quite freely and often produce extensive hybrid swarms. Secondly, to suit his fancy, man, as horticulturist, has selected every conceivable kind of juniper from the great storehouse of natural variation. These unusual and potentially valuable junipers are propagated vegetatively as clones, and where necessary they are grafted to the root systems of sturdy native stock. Many of these variants are hybrids and sometimes contain genes from three or four "species." Usually, these hybrids are not well adapted to the habitats of the species from which they arose, but they may find the going easy either in areas in an early successional stage or in areas moderately disturbed by man's activities. An extensive hybrid swarm may exist in nature for a very long time, and its diversity may be perpetuated, in part at least, by the propagation of clones and spread throughout the world as cultivated plants. Frequently, these horticultural forms are grown in such quantities that sports are occasionally found, and these are then propagated as cultivars. As the result of esthetic impulse man is able to greatly complicate the variation patterns of those species which interest him. It is safe to say that the taxonomy of the junipers is not adequately known and probably will not be until someone is able to look at our wild species as a whole and then fit the cultivated ones into the pattern realistically. It seems probable that when the taxonomy is worked out that there will be fewer named species, more synonyms, more descriptions of the complex variation patterns and analyses of the factors responsible for them.

A review of reproductive behavior will help to point out the nature of the suggested complex variation patterns among junipers. Like many conifers, the juniper habitually produces great numbers of pollen grains and seeds. When the mature pollen is shed in early spring, the plants which bear the staminate cones—containing the pollen sacs—are draped in gold-dust yellow, the color of the millions of pollen grains which are at that time ready to sail like tiny flying saucers and sift into the pollen chambers of the egg-bearing plants.

In most species the berry cones—containing the seeds—are produced, usually each year, on individuals other than those which produce the staminate cones. The abundance of fruit varies considerably from year to year, every third year usually being one of peak productivity. During a year of optimal productivity, a single plant may produce large quantities, tens of thousands, of berry-cones. The number of seeds per berry-cone is usually small. Seed number is relatively constant within a species but between species may vary from one to six. It is obvious that a very large quantity of reproductive material is produced by individual plants, and that in a large population there are as many different potential combinations as there are grains of sand on the ocean floor. In a given population there are approximately equal numbers of pollen-bearing and egg-bearing plants, distributed more or less at random. For a particular egg-bearing plant there may be several pollen-bearing plants at approximately equal distances away. When the pollen is shed, the chances are good that many of the eggs of the egg-bearing plant will be fertilized by pollen from these adjacent trees. However, the eggs do not mature simultaneously but rather over a period of a few days, and some eggs may be fertilized by pollen from plants on an adjacent hillside. Whenever the wind movements are favorable, pollen may be blown from great distances to effect fertilization. Pollen from juniper may be carried several hundred miles. Thus, we see that these junipers possess a great potential variability. This large field of variability is an important contributing factor to the success of these species in disturbed and changing environments.

There are many areas where tremendously variable populations of junipers exist. Where are some of these particularly plastic plants to be found?

Some of the most beautiful junipers in the world are to be found in the broad belt of land known as the Great Plains Province, the region of high prairies or steppes east of the Rocky Mountains. These relatively small, graceful plants are found from the Wichita Mountains of Oklahoma to the Palo Duro Canyon of the Texas Panhandle and farther north from the Black Hills to the foothills of the Rocky Mountains.

There are an amazing number of variations in the junipers within this area of high winds, hot dry summers, and hard winters, and the variations are greater here than in adjacent regions. Why is this so?

These junipers represent the result of the mixing or inter-breeding of two and possibly three species. This two- and three-way hybridizing went on in the distant past, probably in late Pleistocene, when the fluctuations of the flora in response to glaciation and deglaciation evidently caused these species to overlap in distribution. As a consequence of these recombinations of genes, the variability of junipers in this region was greatly increased.

In the Wichita Mountain Wildlife Refuge in southwestern Oklahoma, the species commonly called Virginia juniper or red-cedar, *J. virginiana,* more properly appears to be the result of an ancient mixing of three species. The wild populations and one plantation made by the U. S. Forest Service show evidence that there are present genes of Rocky Mountain juniper, *J. scopulorum,* and of Ashe's juniper or Ozark white-cedar, *J. Ashei.* This mixture produces specimens that are unusual and interesting in color of foliage, thickness of branches, and habit of growth. Many valuable junipers could be selected and bred from the populations on this interesting island of granite in the southwestern Oklahoma prairies.

Farther west in the Palo Duro Canyon of the Texas Panhandle, there are mixtures of red-cedar, Rocky Mountain juniper, and Pinchot's juniper, *J. Pinchoti.* In the northern part of the Great Plains there are a great many hybrids of red-cedar, *J. virginiana,* and Rocky Mountain Juniper, *J. scopu-* lands are a rich source of these variants. One horticulturist, D. Hill of the *lorum,* some of rare beauty. The Platte River country and the Dakota Bad- D. Hill Nursery Company at Dundee, Illinois, was able to find many very valuable types for landscaping purposes by breeding and selecting from these plants of mixed lineage. These organisms of great diversity are often of exceptional value to man. He may select for beauty or utility an almost limitless variety; or he may discover, through controlled breeding, new varieties which otherwise might have remained forever only a potential reality.

Hybrid swarms between *J. Deppeana* and *J. scopulorum* are scattered throughout central and north central New Mexico in the Manzanos and the Sandia Mountains. Some of these with shaggy bark, extra large red fruit, glaucous foliage and graceful branching are eminently suitable for cultivation. Another area where hybrid swarms are quite obvious even to producing bizarre variations is the Walnut Canyon east of Flagstaff, Arizona. I have extensive collections of hybrids from the Canyon involving four species. *J. monosperma* crosses with *J. utahensis, J. scopulorum* and *J. Deppeana; J. utahensis* crosses with *J. Deppeana* and *J. scopulorum.* Hybrids between *J. utahensis* and *J. scopulorum* are frequent from Walnut Canyon north into Utah and east to Mesa Verde.

The historical or geological factors affecting the evolution of junipers, the reproductive behavior, and the forces affecting the distribution of the species relative one to another have produced the complex variation patterns already mentioned. It is no wonder that the classification and phylogeny of junipers is in such a confused and difficult state. It is to be expected. The most aberrant individuals, frequently selected from hybrid swarms, are the ones most appealing to man for cultivation. Before marketing the selected clones, someone names them. These names refer to clones which taken singly may have little significance in the evolution of juniper species, but when considered in terms of overall variation may be extremely significant. It is not at all surprising that many or most of these clones are difficult to relate to the wild types of junipers. Only when the variation patterns of all the junipers are known will it be possible to associate these clones with the right species.

Frequently, plants which represent some recurrent growth form within a species are named as a horticultural variety. Often there are no other characters which are closely correlated with the habit; hence, the one character determines the name of the variety. This procedure is useful to the horticulturist, but it is unrealistic taxonomy. At any rate, whether the horticultural varieties are clones selected from complex populations, growth forms, or other variants, it is frequently difficult to associate them with the species which are often poorly known.

Nature is the greatest experimenter. Throughout the areas where junipers grow, she has been for countless years a plant hybridizer producing horticultural stock, which man has but to select for his use. From nature's laboratory many plants have come which, like the junipers, are rich in variability and may find a wide range of habitats in which to live. These are the strand plants, the transition zone plants, the ecological waifs and weeds whose plastic natures render them almost ubiquitous.

There is almost no significant karyotype differentiation in *Juniperus*. The chromosomes are so similar that crossing is possible between most species, at least within the sections. The timing of the reproductive stages is similar, and most of the species mature their cones in a single season; so that the only real barrier to interspecific crossing is distance. Where the chromosomes have been studied among hybrids, there are few aberrations, an inversion here and a bridge there, suggesting strong gene homology among the species which commonly hybridize. But with this close relationship among the species, there is yet an amazing degree of variability among both vegetative and reproductive characters. The investigator becomes dependent on pattern differences or indices of differences rather than on variations of single characters for differentiating populations. From my experience with *Juniperus,* I feel that ecologic diversification plays the major role in the evolution of races. From the Cretaceous through the Pliocene, there were probably few races or species of *Juniperus*. These were brought together in the Pleistocene glacial fluctuations by climatic shifts and re-adjustments to produce, through hybridization and introgression, ecologic races which further differentiated under the controlling force of selection. Most of the species differentiation in *Juniperus* seems rather recent, and since the settlement of man differentiation has accelerated to an explosive state for many of the recognized species. Some species apparently have had great waves of genic swamping followed by strong selection pressure affecting populations over distances as great as a thousand miles.

KEY TO THE CULTIVATED JUNIPERS ADAPTED FROM REHDER'S MANUAL OF CULTIVATED TREES AND SHRUBS

The following key to the species of *Juniperus* in cultivation in the United States gives one a somewhat false confidence. Those who use the key will still puzzle over a great many specimens from horticultural clones. Some of these species, *J. drupacea, J. Oxycedrus,* and *J. macrocarpa,* are rarely cultivated; most of the species are occasionally cultivated, but a few, like *J. communis, J. chinensis, J. virginiana, J. horizontalis, J. scopulorum,* and *J. Sabina,* are commonly and widely cultivated.

A. Leaves all acicular, ternate, spreading, with 2 white longitudinal lines above (confluent in species 5, 6, 7); winter buds distinct; flowers axillary, dioecious; seeds usually 3.

B. Fruit large, 20 mm. or more across; seeds united into a 3-celled stone; leaves 2½-4 mm. broad, decurrent............Sect. I Caryocedrus Endl.
1. *J. drupacea*

BB. Fruit smaller, 16 mm. or less across; seeds separate; leaves 1-2½ mm. broad, joined directly to the twig (not decurrent)..Sect. II. Oxycedrus Endl.

C. Leaves with the white lines above separated by a green midrib.

D. White line scarcely as broad as the green margin; leaves spreading; branches spreading; cultivated forms shrubby.

E. Leaves very rigid, 12-20 mm. long, tapering from the middle; fruit 6-12 mm. across, rust-red
and polished .... 2. *J. Oxycedrus*

EE. Leaves less rigid, 20-25 mm. long, tapering from the base; fruit 12-15 mm. across often darker and
dull .... 3. *J. macrocarpa*

DD. White lines broader than the green margin; leaves directed forward; branches pendulous; trees .... 4. *J. formosana*

CC. Leaves with white bands mostly confluent.

D. White line narrower than the green margin; leaves grooved above.

E. Upright shrub or tree; fruit 6-8 mm. across; leaves 15-25 mm. long .... 5. *J. rigida*

EE. Procumbent or low shrub; fruit 8-12 mm. across; leaves 10-15 mm. long .... 6. *J. conferta*

DD. White line broader than the green margin; leaves
concave above .... 7. *J. communis*

AA. Leaves all or partly scale-like, rarely all acicular and then decurrent on the twig, ternate or decussate, more or less appressed; without distinct winter buds; flowers terminal on short shoots, dioecious or monoecious; seeds 1-6.
Sect. III. Sabina Endl.

B. Leaves always ternate and acicular.

C. Branches recurved and pendulous; tree .... 8. *J. recurva*

CC. Branches prostrate or spreading; shrub or small tree. . 9. *J. squamata*

BB. Leaves on mature plants wholly or partly scale-like, opposite, opposite and ternate, or mostly ternate.

C. Leaves minutely denticulate (seen with 10X lens).

D. Fruit reddish brown, rather large, fibrous, dry, and bloomy.

E. Scale-like leaves obtuse, opposite; seeds 2-4 . . . . 10. *J. Deppeana*

EE. Scale-like leaves acute, mostly ternate or opposite on the ultimate branchlets; seeds 1-2 . . . . 11. *J. californica* (including *utahensis*)

DD. Fruit blue-black, juicy and bloomy.

E. Leaves conspicuously glandular; fruit with thin skin and flesh; seeds 2-3; usually a tree with single trunk . . . . 12. *J. occidentalis*

EE. Leaves obscurely glandular to glandless; fruit with thick skin and flesh; seeds 1-2; usually shrubby . . . . 13. *J. monosperma*

CC. Leaves entire.

D. Acicular (juvenile) leaves ternate; scale-like leaves obtuse; fruit brown or brownish-purple; seeds 2-3.

E. Scale-like leaves grooved on the back; branchlets very stout . . . . 14. *J. bermudiana*

EE. Scale-like leaves rounded; branchlets fairly slender . . . . 15. *J. chinensis*

DD. Acicular leaves mostly opposite; scale-like leaves acute.

E. Fruit brownish-purple becoming darker, 6-10 mm. across; seeds 5-9; a tree . . . . 16. *J. excelsa*

EE. Fruit blue-black, 3-6 mm. across; seeds 1-6; trees and shrubs.

F. Fruit erect or merely nodding, pedicels straight or nearly so; trees, rarely shrubby.

G. Leaves overlapping, tips acute; glands oval and shorter than the distance from the gland to the leaf tip; trees.

H. Leaves less than 2 mm. long; fruit 3-4 mm. across, wider than long. . . 17. *J. silicicola* (*barbadensis* of American authors)

HH. Leaves 3-4 mm. long; fruit 3.5-6 mm. across, slightly longer than wide . . . . 18. *J. virginiana*

GG. Leaves not overlapping, tips obtuse; glands elliptic and longer than the distance from the gland to the leaf tip . . . . 19. *J. scopulorum*

FF. Fruit pendulous, pedicels sharply recurved; shrubs, often prostrate.

G. Leaves dark green, obtuse or acutish, of strong disagreeable odor when bruised. . . . 20. *J. Sabina*

GG. Leaves bluish green or steel-blue, acute or cuspidate, of aromatic, less strong odor; prostrate shrub . . . . 21. *J. horizontalis*

KEYS TO THE VARIETIES OF JUNIPERS COMMONLY CULTIVATED IN THE UNITED STATES

(Modified from Rehder's Manual)

The keys to varieties work with even less effectiveness than those to species. They will be difficult and frustrating to use for a time, but as one learns the junipers better, they become more easily used and certainly better appreciated for what they are. Except for a few easily identifiable varieties the best means to learn their names is to read the labels—if they happen to have been made up by an expert.

Juniperus chinensis L. This highly variable species shows variation from shrubs less than a meter tall to trees over sixty feet high. Each plant commonly keeps at least some juvenile leaves throughout its lifetime. The scale leaves generally have pale margins. Foliage varies considerably in thickness or heaviness from very coarse to quite fine. Experience suggests that a considerable degree of interspecific hybridization has aided in producing the complex variation in *J. chinensis.*

- A. Plants erect, trees or tree-shaped shrubs at least as tall as wide.
  - B. New growth exposed to the sun suffused with golden yellow . . . . var. *aurea* (Young) Otto
  - BB. New growth not suffused with golden yellow.
    - C. Terminal and main branch tips erect, or at least not conspicuously slanting, nodding or pendulous.
      - D. Acicular leaves inconspicuous, largely confined to scattered twigs.
        - E. Outline various, not conspicuously broad-pyramidal.
          - F. Trees with broadly columnar outline, often conspicuously staminate, rarely with a few scattered fruits . . . . var. *mascula* (Carr.) Rehder
          - FF. Trees with irregular head, not definitely dense and columnar; commonly pistillate . . . . var. *chinensis*
        - EE. Outline conspicuously broad-pyramidal.
          - F. Leaves soft gray-green, somewhat fleshy, obtuse; sprays somewhat flattened, twisted and cristate; plants often staminate . . . . . . var. *Sheppardii* (Veitch) Hornibrook
          - FF. Leaves yellow-green, becoming dark green; sprays not frond-like or cristate; plants pistillate; fruit large, globular, glaucous . . . . var. *Keteleeri* Hort. ex Beissn.
      - DD. Acicular leaves abundant and conspicuous, at least on the lower branches.
        - G. Plants narrowly columnar, 3 times as high as wide, with definite trunk; squamiform leaves only on upper twigs or on a few scattered twigs below . . . . var. *columnaris* Hottes.
        - GG. Plants broader, rarely 2 times as high as wide.
          - H. Juvenile leaves loosely disposed on spreading or moderately ascending twigs; trees with definite trunk.

I. Trees with broadly columnar outlin often conspicuously staminate, rarel with a few scattered fruits . var. mascul

II. Trees with irregular head, not definitel dense and columnar; commonly pisti late . . . . var. *typic*

HH. Juvenile leaves densely packed, on erect c strongly ascending twigs; dense pyramida shrubs without definite axis.

J. Tips of some twigs creamy-white . . . . . var. *variegata* (Maxw. Gordon

JJ. Tips of twigs not variegated . . . . var. *pyramidalis* (Carr.) Rehde

C. Terminal sheet and main branch-tips slanting, nodding or pendulou

K. Leaves mostly acicular, squamiform only on the nodding branch-tips, bright yel low-green . . . . var. *oblonga* (Slavin) Baile

KK. Leaves mostly squamiform, acicular only on inner or lower twigs and branchlet

L. Twigs cord-like, aggregated in mop-like clusters; leaves bright rich green . . . . var. *torulosa* Eastwoo

LL. Twigs somewhat twisted and cristate in appearance, not aggregated in mop like clusters; leaves gray-green; leader and outer branches sparsely twigged . . . . var. *Sheppard*

AA. Plants shrubby, usually broader than high, not tree-like in outline.

M. Lower branches spreading horizontally just above or directly on th ground; plants mat-forming or low and mound-like.

N. Primary branches stout, spreading horizontally above th ground but not prostrate; twigs of adult leaves cord-like an little-branched.

O. Twig-tips not variegated. . . . . . . .var. *Parsonsii* Hornib

OO. Twig-tips, or some of them, creamy-white. . . . . .var. *alba* (Gord.) Rehde

NN. Primary branches slender and prostrate, at least in mature plants twigs of adult leaves, if present, not conspicuously cord-lik

P. Acicular leaves opposite on many conspicuous twig mostly less than 6 mm. long; adult leaves often conspicuous. . . . . .var. *Sargentii* Henr

PP. Acicular leaves apparently all ternate, opposite on few weak inaccessible twigs; squamiform leaves usually lacking.

MM. Lower branches ascending or arching outward well above the groun plants commonly widest at or above the middle.

Q. Twig-tips, or some of them, with conspicuo yellowish variegation, contrasting sharply wit the dark green of the unvariegated portions. . . . . .var. *aurea-variegata* Smit

R. Branch sprays plumose.

S. Plants conspicuously staminat branches spreading or arching outwa at an angle of less than 45°.

T. Leaves mostly acicular or nearly so, commonly grayish-green, aspect more loose and feathery .... var. *Pfitzeriana* (Spaeth) Masters

SS. Plants pistillate; branches of young plants stiffly ascending at more than 45°; aspect of young plants somewhat vase-shaped and stiff, becoming depressed globose with age........... var. *plumosa* Hornibr.

RR. Branch sprays not plumose.

U. Plants soon more than 1 m. tall; main branches one or several, ascending or irregularly inclined, appearing curved and twisted; leaves rich green; twigs cord-like, in irregular mop-like clusters; plants often fruiting conspicuously.................................. var. *torulosa* Eastwood

UU. Plants low, usually to about 1 m. tall, globose or depressed globose in outline; leaves dull or grayish-green; twigs not cord-like; plants staminate.

V. Exposed leaves suffused with golden yellow..... var. *aureo-globosa* Rehd.

VV. Exposed leaves not suffused with golden yellow.... var. *globosa* Hornibr.

Juniperus communis L. Any listing of varieties used in horticulture for this abundant circumboreal species would certainly be arbitrary. About 150 names, mostly based on the naming of clones as varieties, have been given to the variations in *J. communis.* Attempts to group the appropriate names of these into reasonable classes is probably not worth the time. Most of these names are based on very undependable habit differences. I have seen in a single field plants forming mats less than six inches high, prostrate but taller, forming low spreading saucers, forming low cups, and those forming steep-walled funnels. Such fields may be seen in New England, New York, Ontario, Michigan and elsewhere throughout the range of *J. communis* in North America. These fields indicate a great deal of genetic segregation with respect to growth form. Whenever we name clones from such complex material, we are surely somewhat falsely ordering chaos. Even the status of the four commonly known geographical varieties is not clearly understood. However, the following key does suggest the kinds of *J. communis* used in horticulture in this country.

A. Small tree-like plants; branches erect from the base.

B. Main branches erect or ascending, not quite fastigiate, some forms pendulous.. var. *erecta* Pursh

BB. Main branches fastigiate; plants usually columnar.

C. Branchlets erect.

D. Plants to 6 meters, columnar; leaves usually 8-14 mm. long................................. var. *hibernica* Gord.

DD. Plants dwarf, rarely to 1 meter, narrowly columnar; leaves 3-6 mm. long............................. var. *compressa* Carr.

CC. Branches pendulous or, if not, branchlets pendulous.
    D. Branchlets pendulous; tree or shrub, broadly columnar; leaves narrow to 1 mm. wide and 20 mm. long........................var. *oblongo-pendula* Sudw.
    DD. Branchlets not pendulous; branch tips pendulous; leaves 1-½ mm. wide by 12 mm. long, dark green to glaucous.................................var. *suecica* Ait.

AA. Spreading or prostrate shrubs.
  B. Branches ascending, saucer-shaped to cup-shaped in outline, rarely exceeding 1½ meters, leaves straight tapering to a spiny point.
    C. New growth green.........................var. *depressa* Prush.
    CC. New growth yellow......................var. *aureo-spica* Rehd.
  BB. Branches prostrate, rarely exceeding 60 cm. in height; leaves incurved, abruptly pointed.
    C. Branches trailing to 1 meter long and unbranched; leaves linear lanceolate..................................var. *Jackii* Rehd.
    CC. Branches not long trailing and not unbranched; leaves linear oblong.
      D. Leaves concave above, rounded below........var. *saxatilis* Pall.
      DD. Leaves grooved above, kneeled below......var *nipponica* Wils.

Juniperus horizontalis Moench. There is evidence that the Waukegan juniper and those cultivated forms of *horizontalis* from southern Maine are introgressants with different kinds of red-cedar. The var. *Douglasii* (Waukegan) shows characters of the native Wisconsin red-cedar which contains genes of *J. scopulorum.* The ordinary key or synopsis is unavoidably oversimplified, and no key to the cultivated forms will work really efficiently. For example, we say that the var. *horizontalis* is usually green; yet, there are large areas of highly glaucous plants in the Bruce Peninsula and Georgian Bay area of Ontario. In the wild, *J. horizontalis* is frequently found with bushy spots of acicular growth developing from an othewise scale-leaved plant. These spots are usually a response to injury whether by frost, ice, mechanical means, insects, or fungi. When these acicular mounds are propagated they continue to grow indefinitely with the same leaf type and habit. In this way they are very similar to the "retinospora" forms of cultivated conifers. Such peculiar behavior adds to the problems of naming the junipers. The varieties *variegata* and *glomerata* are not popular and are grown mostly as novelties.

A. Branches horizontal, spreading, forming a dense flat-topped mat; leaves acicular; pinkish-violet foliage after frost.......................var. *plumosa* Rehd.

AA. Branches low to ascending, with erect or ascending branchlets; blue to purplish after frost.
  B. Branches ascending, highest at the tips; leaves green, glaucous, mostly acicular...............................var. *alpina* (Loud.) Rehd.
  BB. Branches not ascending to higher tips; leaves green to very glaucous, mostly scale-like.
    C. Branches very short, clustered, without long trailing branches, leaves all scale-like, green..........................var. *glomerata* Rehd.

CC. Branches longer, loose, not clustered, with trailing branches, leaves scale-like and acicular.
  D. Leaves very glaucous, pinkish-blue after frost . . . . .var. *Douglasii* Rehd.
  DD. Leaves mostly green, rarely glaucous.
    E. Branch tips creamy white. . . . . .var. *variegata* Slavin
    EE. Branch tips green. . . . . .var. *horizontalis*

Juniperus Sabina L. There are five varieties in cultivation. Only one, var. *fastigiata,* a small tree, is not commonly cultivated.

A. Small tree, narrowly columnar, with one or more main trunks; dark green scale-like leaves. . . . . .var. *fastigiata* Beiss.
AA. Spreading shrubs.
  B. Low, disk shaped, (1 meter or less), with horizontally spreading branches; leaves mostly acicular. . . . . .var. *tamariscifolia* Ait.
  BB. Bushy to nearly upright, branches ascending, leaves mostly scale-like.
    C. Plants to 2 meters; few acicular leaves; crushed foliage with mild odor. . . . . .var. *von Ehron* Hort.
    CC. Plants to 1½ meters; crushed foliage with very strong odor.
      D. Branch tips often creamy white. . .var. *variegata* (West.) Audib.
      DD. Branch tips green. . . . . .var. *Sabina*

Juniperus scopulorum Sarg. Since the early 1920's horticulturists at the D. Hill Nursery Company at Dundee, Illinois, have been experimenting with interesting clones of the tree forms of *J. scopulorum.* Mr. D. Hill, senior member of the firm, had made a hobby of selecting junipers from the Black Hills of South Dakota, a region of extensive populations of hybrid junipers between *J. scopulorum* and *J. virginiana*. Mr. Hill and his sons have introduced a great many horticultural clones like Hill Silver Juniper, Moonlight, Blue Moon, North Star, Silver Queen, Hill Weeping Juniper. There are over 30 kinds, with only catalogue names, available on the market. Even the better established named varieties are often difficult to identify unless the name tags are on the plants. In correspondence with Dave Hill, he stated that once a *scopulorum* clone left his nursery he would only be able to identify it by reference to the tag. Some of these catalogue plants named above are actually more like *J. virginiana* than *J. scopulorum,* and, indeed, they contain more of the genes of eastern red-cedar. The shrubby forms including catalogue names like *filicinus minimus, lividus, admirabilis, pulchellus, adpressus* and *planifolius, Parkii* may all be hybrids between *J. scopulorum* and *J. horizontalis.* This is evidently true of the var. *repens* and *Careei* which are lumped together under var. *patens* Fassett.

A. Small trees.
  B. Leaves green (or slightly glaucous in var. *scopulorum*).
    C. Foliage dark green. . . . . var. *scopulorum*
    CC. Foliage bright green. . . . . var. *viridifolia* D. Hill
  BB. Leaves very glaucous. . . . . var. *argentea* D. Hill
AA. Low shrubs forming a mat or a cup-like growth. . . . . var. *patens* Fassett

Juniperus squamata Lamb. The var. *squamata* and var. *Fargesii* are mostly to be found in botanical gardens and are little used in landscaping. The var. *Wilsonii* is apparently a novelty known in the Arnold Arboretum and rarely elsewhere. But the var. *Meyeri* is a highly favored plant for landscaping.

A. Prostrate or spreading shrub .... var. *squamata*
AA. Trees or shrubs taller than wide.
B. Trees .... var. *Fargesii*
BB. Shrubs.
C. Leaves green; dense mound-like plants to 2 meters; branches recurved at tips .... var. *Wilsonii* Rehd.
CC. Leaves glaucous; irregular upright shrub; branches ascending and straight .... var. *Meyeri* Rehd.

Juniperus virginiana L. This species is very complex because of introgressive hybridization with other species (or subspecies) with which it is or was in contact. The variation in red-cedar shows fairly clear geographic trends. From the Ozark Plateau southwestward there are the broader bushy forms which are introgressants with *J. Ashei* of the Edwards Plateau in central Texas. From the Texas panhandle north to Iowa, Wisconsin, Nebraska and South Dakota there are many small tree forms with wand-like, beautifully strict, branches which fruit very heavily. These are introgressants of *J. scopulorum* into *J. virginiana.* From the Gulf coastal plain of Texas to Florida and north inland to the Atlantic coastal plain to southern North Carolina there are fairly large tree forms with fine foliage and small fruit. These are apparently introgressants of *J. lucayana* into *J. virginiana.* In the north the oldest native red-cedars tend to be either crebriform or at least fairly narrowly columnar. There are a few low forms from the north particularly var. *ambigens* which is a hybrid between *J. virginiana* and *J. horizontalis.* Red-cedar contains a wealth of variation from which aberrant or interesting plants may be selected for horticultural purposes.

A. Plants variegated (color forms), trees.
B. New growth white, older growth green; mostly acicular leaves; habit pyramidal .... var. *plumosa* Rehd.
BB. New growth white to gold and green at once.
C. Branches white or creamy white variegated .... var. *albo-spica* Beiss.
CC. Branches yellow variegated .... var. *elegantissima* Hochst.
AA. Plants green or glaucous; trees and shrubs.
B. Leaves green.
C. Trees.
D. Branches from the base of very indefinite main axis; leaves dark green .... var. *pyramidiformis* D. Hill
DD. Branches regular on the main axis.
E. Branch tips nodding; branchlets pendulous .... var. *pendula* Carr.

EE. Branch tips straight; branchlets not pendulous.
F. Plants strictly columnar; branches very dense .... var. *pyramidalis* Carr.
FF. Plants broader, 2-3 times taller than wide; branches mostly less dense.
G. Leaves mostly acicular, bright green, purplish after frost; branches very dense. .var. *Hillii* Hort.
GG. Leaves mostly scale-like; plants green or bronze, never purple.
H. Trees, columnar with ascending branches; plants green, sometimes bronze in winter ....var. *crebra* Fern. and Grisc.
HH. Trees small, compact, pyramidal; plants dark green or yellow green, not bronzing.
I. Leaves dark green; plants with glaucous fruit, fruiting profusely........ var. *Canaertii* Sénécl.
II. Leaves bright yellow green; not fruiting profusely .... var. *Schottii* Gord.
CC. Shrubs.
D. Plants globose; leaves bright green, scale-like .... var. *globosa* Beiss.
DD. Plants spreading; leaves green or gray-green, acicular or scale-like.
E. Leaves mostly acicular, green; branches stiff, tips and branchlets suggesting three growth planes .... var. *tripartita* Sénécl.
EE. Leaves mostly scale-like; plants less than 1 meter tall.
F. Plants mat-like; branching at a single level .... var. *ambigens* Fassett
FF. Plants mound-like; branching at several levels .... var. *Kosteri* Beiss.
BB. Leaves quite glaucous, trees.
C. Habit narrowly pyramidal.
D. Leaves bluish-white; a staminate clone.......var. *Burkii* Hort.
DD. Leaves grayish-white; a pistillate clone .... var. *venusta* (Ellw. & Barry) Rehd.
CC. Habit broader, open; leaves bluish-white, often fruiting profusely .... var. *glauca* Carr.

BIBLIOGRAPHY

Antoine, F. 1857. Die Cupressineen—Gattungen: *Arceuthos, Juniperus* and *Sabina.* Vienna.

Antoine and Kotschy. 1854. *Arceuthos* in Oestr. Bot. Wochemblat IV.

Buchholz, J. T. 1948. Generic and subgeneric distribution of the Coniferales. Bot. Gaz. *110:* 80-91.

Dallimore, W. and A. B. Jackson. 1948. A handbook of Coniferae. Third Edition. Edward Arnold and Co., London.

Endlicher, S. 1847. Generum Plantarum Supplementum Quartum, Pars. II.

Kaiser, Margaret. 1954. A report on the mature wood of the Syrian or drupe-fruited juniper, *Juniperus drupacea* Labill. Amer. Mid. Nat. *51:* 306-310.

Labillardière. 1791. *Juniperus drupacea* in Pl. Syr. Decad. II.

Pilger, R. 1926. Coniferae, in Engler and Prantl, Die Natürlichen Pflanzenfamilien. Second Edition. Leipzig.

Rehder, A. 1940. A manual of cultivated trees and shrubs hardy in North America. Second Edition. Macmillan, New York.

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